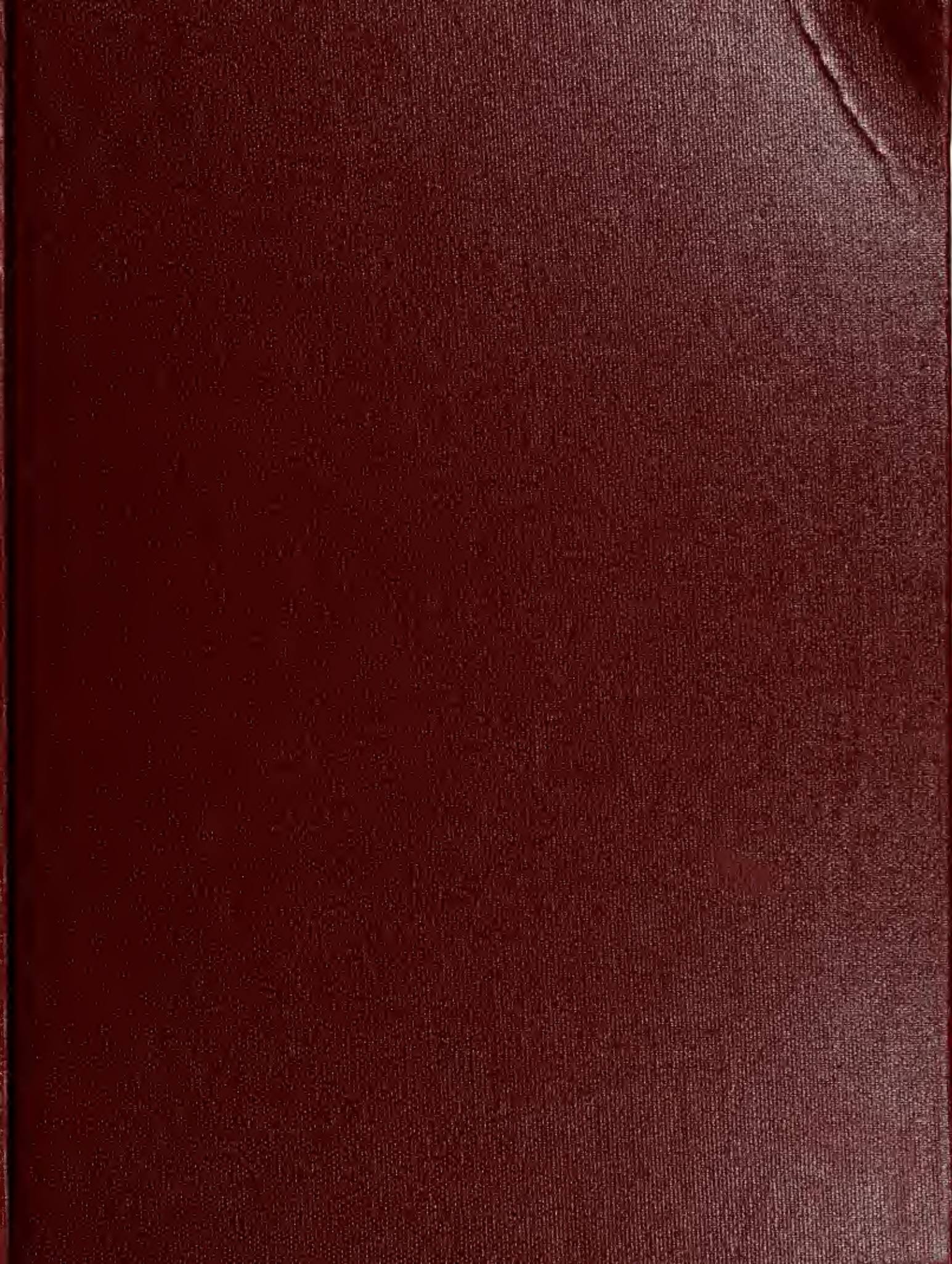




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Three Species in the *Vipera kaznakowi* Complex (Eurosiberian Group) in the Caucasus: Their Present Distribution, Possible Genesis, and Phylogeny†

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Abstract.—Three valid species: *Vipera kaznakowi* Nikolsky, *V. dinniki* Nikolsky and *V. darevskii* Vedmedeja, Orlov, and Tuniyev of the "*Vipera kaznakowi*" complex belonging to the Eurosiberian viper group are recognized. The distributions of the closely related species, *V. kaznakowi* and *V. dinniki* are defined. The habitat of *V. kaznakowi* is present along the Black Sea coast, from Khopa Village (Turkey) in the south, to Maikop (USSR) in the north. *Vipera kaznakowi* is associated with montane areas from sea level up to 1000 m. The range of *V. dinniki* covers the northern and southern slopes of the Great (Main) Caucasus Ridge, ranging from the Fisht-Oshten Massive in the west to Shkhara Mountain in the east. *Vipera dinniki* tends to be restricted to alpine and subalpine zones at elevations from 1500 m to 3000 m. *Vipera darevskii* occurs in the southeastern part of the Dzhavachet Mountain Ridge, Armenia, near the border with Georgia. The history of studies on the vipers of the "*Vipera kaznakowi*" complex is summarized. The possible genesis of the present distributions of these vipers and their phylogenetic relationships are discussed. Comparative morphological and ecological characters of the three species are listed.

Key Words: Reptilia, Serpentes, Viperidae, *Vipera*, USSR, Caucasus, systematics, ecology.

Introduction

The study of the following viper species of the Caucasus, *Vipera kaznakowi* Nikolsky 1909, *V. dinniki* (Nikolsky 1913), and *V. darevskii* Vedmederja, Orlov and Tuniyev 1986 and the history of their distributions is of great interest for understanding the phylogenetic links of the Eurosiberian shield-headed vipers from the Caucasus (subgenus *Pelias*, Merrem 1808) and the formation of the present snake fauna in the west Caucasus Isthmus.

Ever since Nikolsky (1909) described the Caucasus Viper, *Vipera kaznakowi*, the understanding of the taxonomic position of this species has constantly varied. Also, ideas regarding the habitats of those forms referred to this species have varied (Orlov and Tuniyev 1986). We recognize at least three closely related species within the *V.*

kaznakowi complex. All of them occur primarily in the western part of the Caucasus Isthmus. The eastern boundary of the species range needs to be defined. The Caucasus vipers (Fig. 1) have been recorded from the following localities:

Western Dagestan in the vicinity of Khasav-Yurt (Krasovsky 1929, 1932).

Along the slope of Makh-khokh Mountain from the highlands of Ingushetia (Chernov 1929).

On Legli Mountain in the Gukasyansky region, Armenia (Darevsky 1956).

In the vicinity of Ushguli at the foothills of Shkhara Mountain in Svanetia, Georgia (Muskhelishvili 1959).

In Borzhomi Canyon, Georgia (Bakradze 1969, 1975; Bannikov et al. 1977).

In Lagodekhi, Georgia (Zoological Institute, the USSR Academy of Sciences, Nos. 8389 and 13769).

† This publication combines material previously published in Russian by Orlov and Tuniyev (1986) and Vedmederja et al. (1986) with additional information.

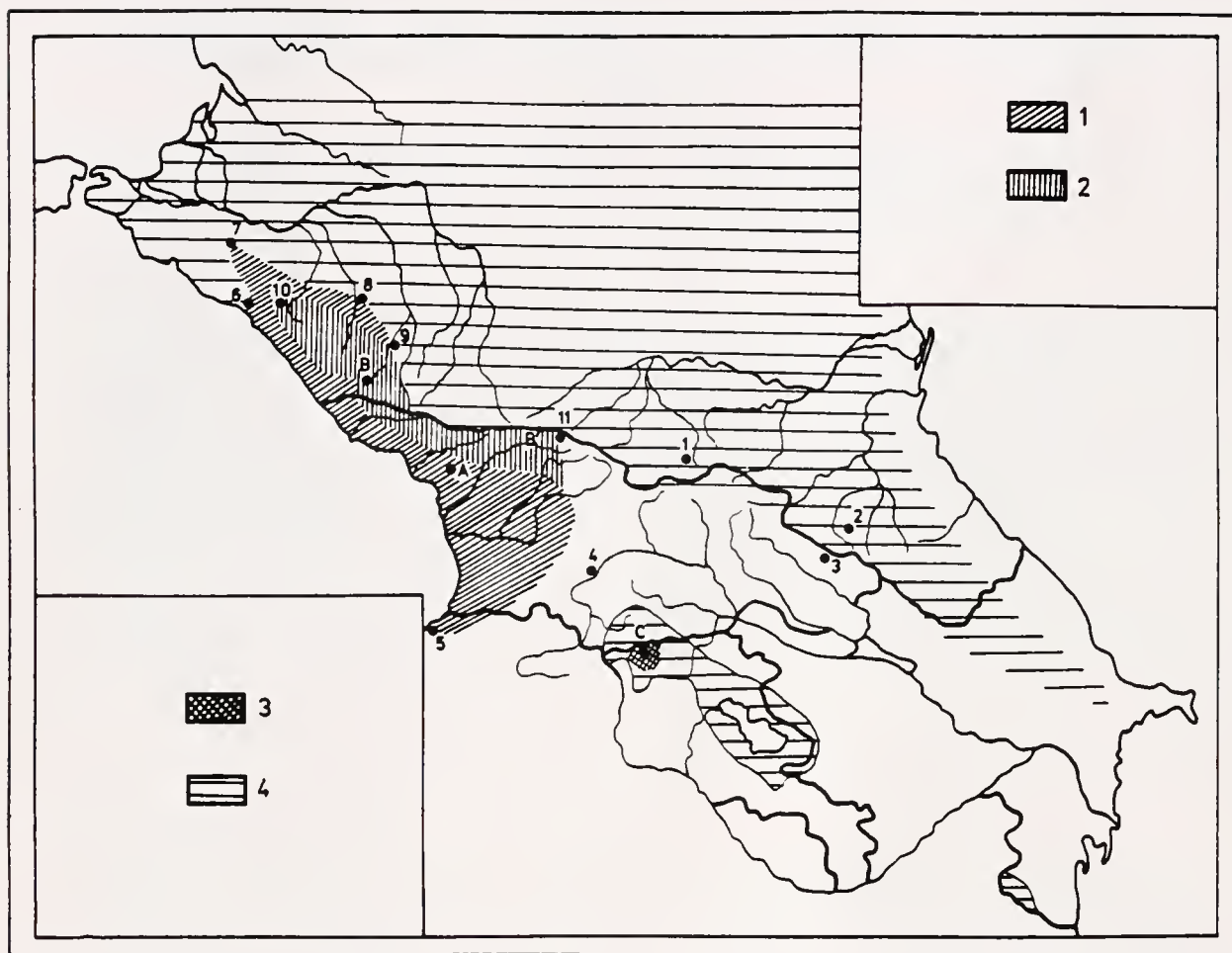


FIG. 1. The distributions of the vipers from the *Vipera kaznakowi* complex and the *Vipera ursini* complex in the Caucasus. 1. *V. kaznakowi*, 2. *V. dinniki*, 3. *V. darevskii*, 4. *V. ursini renardi* (northern population) and *V. ursini eriwanensis* (southern population). Type localities: A—*V. kaznakowi*; B, B'—*V. dinniki*; C—*V. darevskii*. Localities: 1—Makh-Khokh Mountain; 2—the settlement of Khasav-Yurt; 3—Lagodekhi; 4—Benis-Kheri Canyon; 5—the settlement of Khopa, Turkey; 6—Mikhailovsky Pass; 7—the settlement of Ubinskaya; 8—the town of Maikop; 9—the mouth of the Urushten River; 10—the Fisht-Oshtenovskiy Massive; 11—Shkhara Mountain. Extreme points of the distributions are marked.

All three species, *Vipera kaznakowi*, *V. dinniki* and *V. darevskii*, differ in morphology and ecology (Vedmederja 1984; Orlov and Tuniyev 1986).

History of the study of the Vipera kaznakowi complex.

The taxonomic problems and interrelationships of the viper forms of the Eurosiberian group in the Caucasus has caused contradictions and has confused zoologists for nearly a hundred years. The fragmented highland landscapes within the

overall range of the Caucasus vipers isolates even neighboring populations. Hence, there is an accumulation of unique characteristics in populations. Very complex situations emerge in sympatric areas of closely related species of this complex. This may be connected with natural hybridization. Occasionally the identification of some individuals from intergrading populations is difficult. This particularly concerns *Vipera dinniki* in the areas of its interactions with *V. kaznakowi*, and additionally with the vipers of the *V. ursini* complex (Bonaparte). The high

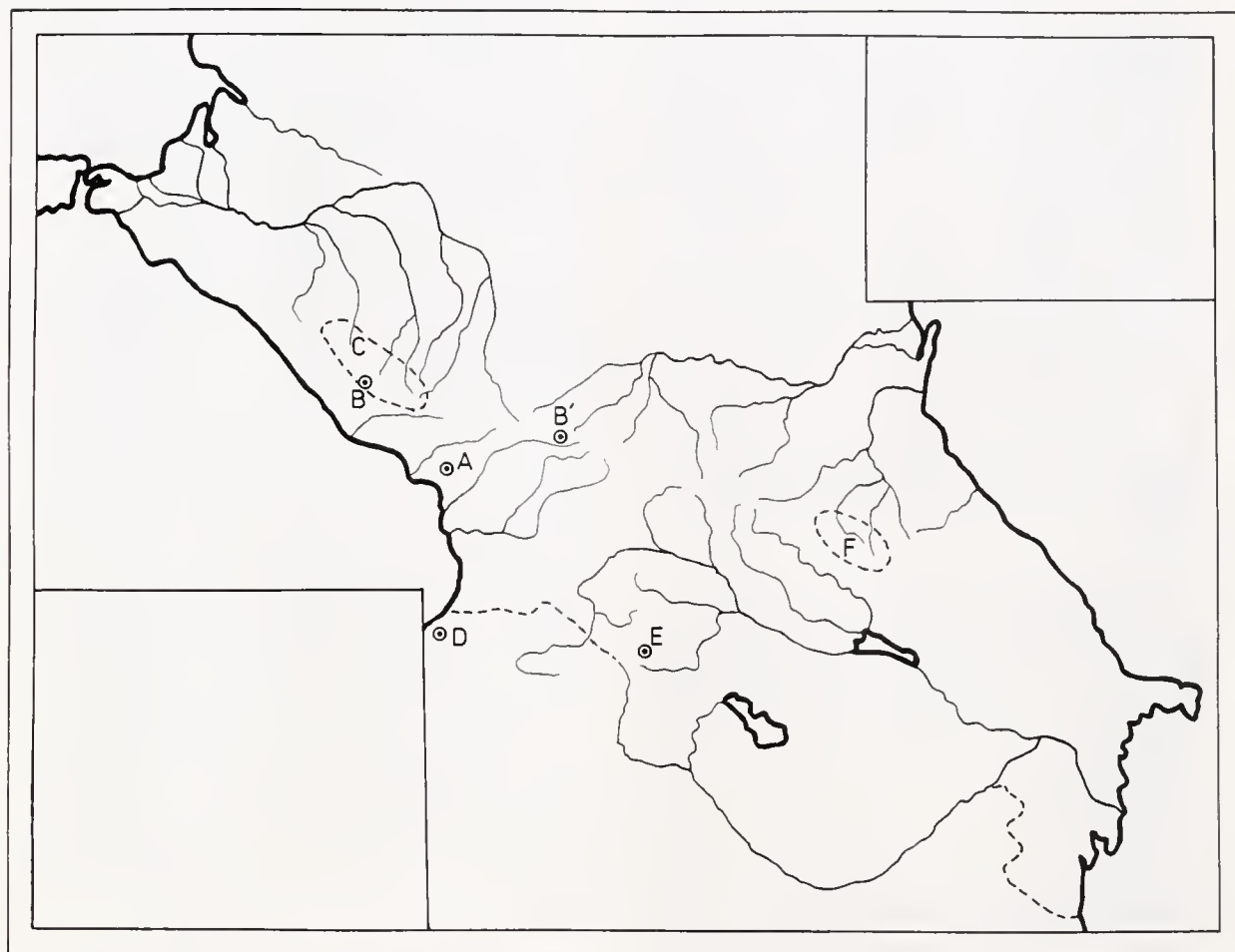


FIG. 2. Type localities of the vipers of the *Vipera kaznakowi* complex proposed over the history of the study. A – *V. kaznakowi* Nikolsky, described in 1909, collected from Tsebelda, the vicinity of Sukhumi, Abkhazia, Georgia. B, B' – *V. Berus dinniki* Nikolsky, described in 1913, from the upper reaches of the Malaya Laba River, the Caucasus Reserve, Krasnodarsky Territory and Svanetia, Georgia (respectively). C – *V. tigrina* Tzarewsky, described in 1916, taken from the Northern Caucasus. D – *V. berus ornata* Basoglu, described in 1947 from the settlement of Khopa, Artviisky Vilayet, Turkey. E – *V. darevskii* Vedmederja, Orlov, and Tuniyev, 1986, from Legli Mountain, the Mokrye Mountains, Gukasyansky Region, Armenia. F – *V. kaznakowi orientalis* Vedmederja, 1984 from the eastern part of the Main Caucasus Ridge.

degree of phenotypic polymorphism in vipers from the *V. kaznakowi* complex also creates additional problems in the evaluation of their taxonomic position.

Due to the complexity in identification of these vipers and the absence of definite localities for specimens an analysis of old literature gives only an approximate idea regarding the relationships of the *Vipera kaznakowi* complex.

Rossikow (1890) mentioned "multi-

colored" vipers in the Northern Caucasus defined as *Vipera berus*. Boettger (1893) regarded the dispersal of two closely related viper species, *V. berus* and *V. renardi* from the Caucasus as a phenomenon that deserves attention. Nikolsky (1905) considered *V. berus* to be associated with Transcaucasia whereas *V. renardi* inhabits steppe areas of the Precaucasus and mountains of the Northern Caucasus. Leister (1908a) in his sketch on the geographic distribution of *V. renardi* and *V. berus* within the Caucasus wrote that *V.*

renardi is associated with steppe areas which separate the Caucasus from the habitat of *V. berus*, and also the mountains of the Northern Caucasus. He also confirmed Boettger's and Nikolsky's opinions that *V. berus* also appears in Transcaucasia. In the northern Transcaucasia there is an isolated population. According to Boettger (1899), the individuals of *V. berus* which are preserved at the Caucasus Museum (now the Museum of Georgia) were collected from Suani, Tiflis, Avar, Kodzhori, Khasav-Yurt, and Kazikoparan, whereas those from the Senckenburg Museum (Frankfurt-am-Main, West Germany) were taken from Sukhumi, Georgia.

Leister (1908a,b,c) gives a list of *Vipera berus* specimens in the collection of the Zoological Museum of the Academy of Sciences (now Zoological Institute of the USSR Academy of Sciences) taken from the Caucasus: 1) from Tiflis and Lagodekhi regions, Georgia and 2) from Yelenovka near the Gochka Lake (now the Sevan Lake). Leister then states that he found *V. renardi* on the bank of the Gochka Lake at the same locality where Kessler and Brandt collected *V. berus* (this specimen, ZIN 5478, collected by Brandt we determined to be *V. ursini*). On the basis of the findings of Kessler and Brandt and his own findings, Leister comes to the conclusion that both species, *V. berus* and *V. renardi*, live sympatrically. Concerning the specimens collected by Kessler and Brandt, Nikolsky (1905) writes that their rostral touches only one apical scale like in *V. renardi*. In all other characters they look more like *V. berus*. This led Leister (1908a) to consider that a certain intermediate species is possible—an ancestral form of *V. berus* and *V. renardi*. Nikolsky (1913) referring to the vipers from Transcaucasia listed by Kessler, Brandt and Leister nevertheless concluded that they are *V. renardi*. Leister (1908a,b), having analyzed the collections, concludes that the territory of the Northern Caucasus and Transcaucasia are inhabited by *V. berus* and *V. renardi*. He thought that *V. berus* and *V. renardi* live sympatrically in the Northern Caucasus (for instance, the

vicinity of Grozny is a sympatric area).

Since Nikolsky (1909) described *Vipera kaznakowi*, a number of synonyms have been proposed for this species as new forms have been described and new combinations proposed. A number of forms, primarily from the Northern Caucasus and from the eastern range of *V. kaznakowi* have confused taxonomists as to their relationship to *V. kaznakowi*. These forms were placed in different combinations within *V. berus* and *V. ursini* (Nikolsky 1913, 1916; Basoglu 1947; Knoepfler and Sochurek 1955; Kramer 1961). Nikolsky (1913) assigned the common Caucasus viper to a new subspecies, *V. berus dinniki*. He defined the viper's range as the northern and southern slopes of the Caucasus Ridge from the Malaya (Small) Laba River headwaters up to Elbrus Mountain. Morits (1916) also recorded *V. berus* in the Northern Caucasus. Tsarevsky (1916) described a new form *V. tigrina* that was closely related to *V. renardi* and *V. kaznakowi*. Unfortunately he cited the species locality solely as "the Northern Caucasus."

Nikolsky (1909, 1911, 1913, 1916), the author of *Vipera kaznakowi* and *V. berus dinniki* descriptions, studied the relationships of the species *V. kaznakowi*, *V. berus*, and *V. renardi* (= *V. ursini renardi*) and noted the difficulties in identification of these forms. Nikolsky (1913) described *V. berus dinniki* from a single specimen collected by N. Y. Dinnik at the upper reaches of the Malaya Laba River, and from three specimens found by Shelkovnikov in Svanetia, Georgia. In his next monograph, Nikolsky (1916) discussed both forms: *Coluber berus dinniki* and *Coluber kaznakowi*. The range of the former was defined as the Caucasus Mountains on both sides of the Great Caucasus Ridge. The upper reaches of the Bolshaya (Big) Laba River was designated as a sympatric zone for *V. berus dinniki* and *V. renardi*. In his opinion, *V. renardi* was closely associated with the Caucasus Black Sea coast and the northern slope of the Caucasus Ridge.

Dinnik (1926) noted that *Vipera berus* and *V. kaznakowi* occurred in the Northern Caucasus. Krasovsky (1929) indicated that *V. berus* inhabited Khasav-Yurt and Rutulsky Kanton, Dagestan. Chernov (1929) recorded *Coluber berus dinniki* in the highlands of Ingushetia on the southern slope of Makh-khokh Mountain. The specimens were collected by D. Krasovsky in 1926 (Fig. 1). Krasovsky (1933) included both *V. kaznakowi* and *V. berus* in the fauna of the Caucasus State Reserve. Bartenev and Reznikova (1935) concluded that *V. kaznakowi* and *V. berus dinniki* were distributed in the western Caucasus, whereas in the alpine, *V. ursini renardi* also occurred. Rostombekov (1939) recorded *V. kaznakowi* as part of the fauna of Abkhazia. A new form, *V. berus ornata*, was described from northeast Anatolia (Basoglu 1947). Later on Mertens (1952a) synonymized it with *V. kaznakowi*. Terentyev and Chernov (1949) regarded *V. tigrina* Tzarevsky and *V. berus dinniki* Nikolsky as junior synonyms of *V. kaznakowi* Nikolsky which is, in their opinion, related to *V. ursini renardi*.

Darevsky (1956) presented a new combination of names for the viper from the Gukasyansky region, Armenia: *Vipera ursini renardi*. Fyodorov (1956) recorded *V. berus* in the forests of the premontane area of the Stavropolsky Territory and *V. kaznakowi* in the subalpine belt. In his survey of the snake fauna of Abkhazia, Georgia, Milyanovsky (1957) mentions *V. kaznakowi*. Muskhelishvili (1959) records *V. kaznakowi* on Mount Shkhara from the vicinity of Ushguli, Svanetia, Georgia. Kramer (1961) regards *V. tigrina* a junior synonym of *V. kaznakowi*, whereas *V. berus dinniki* should be synonymized with *V. ursini renardi*. Bakradze (1969) found a female *V. kaznakowi* in the town of Banis-Khevi, near Borzhomi, Georgia. On the basis of this finding, he suggested that the species habitat covered the entire Adzharo-Imeretinsky Ridge and some of the Trialetsky Ridge.

In the field guide of Bannikov et al. (1977) the names *Vipera berus dinniki*, *V.*

tigrina and *V. berus ornata* are mentioned as junior synonyms of *V. kaznakowi*. Vedmederja (1977) recorded *V. kaznakowi* in Adgaria, Georgia. In his opinion (Vedmederja 1984) *V. kaznakowi* is a polytypic species comprising four subspecific forms. Tertyshnikov (1977), in defining ecological and zoogeographic subdivisions of the herpetofauna of the Northern Caucasus, noted that *V. kaznakowi* tends to be restricted to western and southwestern montane regions. The most recent taxonomic works dealing with these vipers state that *V. berus* occurs neither in the Caucasus nor in the Precaucasus. Hence, *V. kaznakowi* is the sole valid name with regard to shield-headed vipers from the western Caucasus Isthmus and northeast Anatolia. The taxonomic status of the eastern populations from Dagestan and Armenia was not discussed (Terentyev and Chernov 1949; Mertens 1952a; Mertens and Wermuth 1960; Klemmer 1963; Bannikov et al. 1977; Baran 1977; Harding and Welch 1980).

The study of old collections and literature shows that the majority of researchers did differentiate the vipers from the *Vipera ursini* complex and the *V. kaznakowi* complex. The major difficulties in defining the systematic position and taxonomic status concerned primarily the vipers from the eastern range of the *V. kaznakowi* complex. References that *V. berus* occurs in the Northern Caucasus and Transcaucasia more often than not concern snakes from the *V. kaznakowi* complex rather than those from the *V. ursini* complex.

An analysis of literature data and morphometric characteristics of 141 viper specimens allowed Vedmederja et al. (1986) to designate three species within the *Vipera kaznakowi* complex:

1. *V. kaznakowi* Nikolsky, 1909
2. *V. dinniki* Nikolsky, 1913
3. *V. darevskii* Vedmederja, Orlov and Tuniyev, 1986

Fig. 2 represents type localities of the forms proposed for the *Vipera kaznakowi* complex over the history of its study.

Systematic Accounts

Vipera kaznakowi Nikolsky, 1909
(Fig. 3, 4, 14a, Plate 1)

Chronology of species description

Vipera renardi (Christoph) - Silantyev, 1903, 30:37 (part).

Vipera kaznakowi Nikolsky, 1909:174; Nikolsky, 1910:81, table 1.

Vipera kaznakowi - Nikolsky, 1913:179-181; colored plate III (=Fig. 3, this paper).

Coluber kaznakowi - Nikolsky, 1916:244-247.

Vipera berus ornata Basoglu, 1947:182-190.

Vipera ursini kaznakowi - Knoepfler and Sochurek, 1955:185-188.

Vipera kaznakowi - Terentyev and Chernov, 1949:270-277 (Map 15); Bannikov et al., 1977:323-324 (map 133; colored plate 31, 4).

Vipera kaznakowi kaznakowi - Vedmederja, 1984:8.

The English common name is the Caucasus Viper, or Kaznakow's Viper.

Lectotype[†]: No. 4408, an adult female. Collected by Y. V. Voronov from Tsebelda, the vicinity of Sukhumi, Abkhasia, the Caucasus. It is stored in the Caucasian Museum (now the Museum of Georgia, Tbilisi).

Diagnosis: A large snake for the Eurosiberian group. Total length reaches 650-700 mm. Dorsally the head is covered with large scales. In size and shape they differ considerably from body scales. Nostril is cut through either in the middle or slightly closer to the lower edge of the nasal. Upper-lateral edge of snout is pointed. Rostral normally reaches two apical scales on upper snout. Upper edge of the nasalarostror scale is slightly curved at obtuse angles. Scales of anterior frontal have weak longitudinal keels. Head is broad and normally black dorsally. Head is separated from body by a sharp nuchal collar.

Description: The ratio of body length to tail length is 5.7 to 6.4 in males and 7.5 to 10.9 in females. Unlike other species assigned to the *Vipera kaznakowi* complex, red and yellow colors prevail in *V. kaznakowi*. Melanistic specimens are common. However, unlike complete melanistic individuals of *V. dinniki*, those of *V. kaznakowi* preserve yellow or red color on either upper or lower labials. *Vipera kaznakowi* is either black or dark brown striped dorsally and laterally. Often stripes merge so that only red or yellow spots remain between them. Ventrums are black. Head is very broad, impressed dorsally. This fact is emphasized by a slightly pointed upper edge of snout. Cheeks are greatly swollen. Head is well separated from body by a thin nuchal collar. Comparative data on scalation and size characters are listed in Tables 1-4.

Variability and comparative remarks

V. kaznakowi (Fig. 4, Plate 1) is undoubtedly more closely related to *V. berus* and *V. ursini*. Supposedly, when interacting with *V. ursini renardi* and *V. ursini eriwanensis* it forms two species of hybrid genesis: *V. dinniki* and *V. darevskii*. From all listed forms it differs by: 1) the extraordinarily great width of the triangular head, 2) the head width of specimens of this species equals the distance between tip of snout and posterior angle of mouth slot, 3) the "cheeks" are greatly swollen, hence a broad furrow

[†] Kramer (1961) was mistaken regarding this specimen as the holotype, because Nikolsky (1909) had not singled out a holotype from the five specimens from which he described the species.

Nikolski. Nova species viperae.

Изв. Кавк. Муз. Т. V.



A. J. E. Torzi del.

И. Казнаков С. Д. Е.

Vipera kaznakovi sp. n.

FIG. 3. Type specimen of *Vipera kaznakovi* Nikolsky, 1913 (reproduced from Plate III, originally printed in color, Nikolsky 1913).

TABLE 1. Comparative scale characters of the three viper species of the "*Vipera kaznakowi*" complex.

Species Characters	<i>Vipera kaznakowi</i>			<i>Vipera dinniki</i>			<i>Vipera darevskii</i>		
	n	min-max	$\bar{x} \pm se$	n	min-max	$\bar{x} \pm se$	n	min-max	$\bar{x} \pm se$
1. Number of scales round the eye	64	8-12	10.03 $\pm$ 0.1	65	9-12	9.6 $\pm$ 0.1	9	8-9	8.4 $\pm$ 0.2
2. Number of upper labials	64	8-10	9.0 $\pm$ 0.1	68	8-11	10.3 $\pm$ 1.3	9	9-10	9.2 $\pm$ 0.1
3. Number of lower labials	64	8-12	10.9 $\pm$ 0.05	68	8-12	10.5 $\pm$ 0.1	9	9-10	9.5 $\pm$ 0.2
4. Number of ventrals	64	130-143	135.5 $\pm$ 0.8	68	126-141	133.9 $\pm$ 1.8	9	134-140	135.5 $\pm$ 0.8
5. Number of scale rows around body	64	18-21	20.0 $\pm$ 0.1	68	21-23	21.1 $\pm$ 0.15	9	19-21	20.6 $\pm$ 0.2

TABLE 2. Sexual dimorphism of body length and number of subcaudals in the three viper species of the "*Vipera kaznakowi*" complex.

Characters	♂ ♂			♀ ♀			t ♂ ♀	p
	n	min-max	x±se	n	min-max	x±se		
<i>Vipera kaznakowi</i> :								
Body length	23	358-475	415.1±7.5	16	375-600	504.1±118.6	4.5	<0.001
Number of subcaudals	23	31-40	34.8±1.5	20	22-32	25.4±0.9		
<i>Vipera dinniki</i> :								
Body length	29	259-412	331±8.76	20	321-486	441.8±11.4	5.6	<0.001
Number of subcaudals	29	31-37	32.2±0.6	20	18-30	23.7±0.8		
<i>Vipera darevskii</i> :								
Body length	3	236-258	249.3±5.53	5	233-421	331.8±28.2	2.82	<0.05
Number of subcaudals	3	29-35	32.3±1.4	5	25-30	27±0.79		

TABLE 3. A comparison of the number of vertebrae carrying ribs in Shield Headed Vipers of the USSR. X-ray analysis of the vipers indicates that the number of rib-carrying vertebrae is stable, except for *Vipera dinniki*, (indicated by **) in which the number varied from 128 to 140.

Specific and subspecific viper forms	Number of specimens analyzed	Number of rib bearing vertebrae
<i>Vipera berus</i>	10	142
<i>Vipera kaznakowi</i>	8	135
<i>Vipera darevskii</i>	9	138
<i>Vipera dinniki</i>	25	138**
<i>Vipera ursini renardi</i>	10	148
<i>Vipera u. eriwanensis</i>	10	140
<i>Vipera dinniki</i>	2	132 and 135

appears between eye and temple. The furrow goes up to upper head, parallel to upper edge of parietals. Dorsally the head is either impressed or flat. The viper also differs from closely related species in body proportions: 1) it is relatively thicker, more

massive; 2) the head is conspicuously bigger. These habitus characters differentiate all age groups of *V. kaznakowi* ranging from juveniles to mature specimens. Comparative data on pholidosis, size, and number of vertebrae

TABLE 4. Comparative morphology of vipers in the "*Vipera kaznakowi*" complex.

<i>Vipera kaznakowi</i> , 64 specimens	<i>V. dinniki</i> , 68 specimens	<i>V. darevskii</i> , 9 specimens
● SVL ♂♂ ≠ 475 mm	● SVL ♂♂ ≠ 412 mm	● SVL ♂♂ ≠ 258 mm
SVL ♀♀ ≠ 600 mm	SVL ♀♀ ≠ 486 mm	SVL ♀♀ ≠ 421 mm
● SVL ♂♂ / CL ≈ 5.6-6.4	● SVL ♂♂ / CL ≈ 5.9-7.4	SVL ♂♂ / CL ≈ 6.0-6.5
SVL ♀♀ / CL ≈ 7.5-10.9	SVL ♀♀ / CL ≈ 7.9-13.5	SVL ♀♀ / CL ≈ 8.4-9.3
● Head is either impressed or flat dorsally	● Head is either flat or slightly protuberant dorsally	● Head is either flat or slightly protuberant dorsally
● Edge of snout is slightly rounded	● Edge of snout is rounded	● Edges of snout are slightly pointed laterally. Anterior edge is a little rounded
● Rostral is broad. Usually touches two apical scales (in 91% specimens) rarely one apical (in 9%)	● Rostral is narrow reaching either one (in 48.6%) or two (in 51.4%) apicals	● Rostral is more narrow and touches one (in three specimens) or two (in six specimens) apical scales
● The width of the frontal is equal to 1.21-1.72 of its length	● The width of the frontal is equal to 1.13-1.83 of its length	● The width of the frontal is equal to 1.48-1.71 of its length
● The distance between anterior edge of the frontal and the rostral is equal to 0.75-1.05 of the frontal edge	● The distance between anterior edge of the frontal and the rostral is equal to 0.77-1.35 of the frontal edge	● The distance between anterior edge of the frontal and the rostral is equal to 0.67-1.07 of the frontal edge
● Frontal is either smaller than parietals or equals them	● Frontal is either smaller than parietals or equals them	● Frontal is larger than parietals
● Large lower oculars are separated from frontal either by one row (in 87.0%) or rarely by two rows of small scales (in 12.4%)	● Large lower oculars are separated from frontal either by one row (in 58.5%) or two rows (in 41.5%)	● Large lower oculars are separated from frontal only by a single row of small scales (in all nine specimens)
● The upper pre-ocular does not touch the nasal in 96.1%. In 3.9% it does	● The upper pre-ocular does not touch the nasal in 86.6%. In other cases it reaches the nasal	● The upper pre-ocular does not touch the nasal in two specimens. In seven specimens it does
● Nostril is either cut through in the middle of nasal or is slightly shifted downwards	● Nostril is cut through in the center or nasal. It may be shifted downwards exceedingly rarely	● Nostril is cut through in the lower part of the nasal
● Nasal does not touch rostral	● Nasal does not touch rostral	● Nasal does not touch rostral
● Body scales with expressed keels; some scale rows that reach ventrals have no keels	● Body scales have expressed keels. 76% of scales that reach ventrals have no keels, 18.4% have slightly expressed keels, 5.6% have well-expressed keels	● Body scales have expressed keels. Some scale rows that reach ventrals have no keels

supporting ribs are given in Tables 1-4.

Coloration. *Vipera kaznakowi* are incredibly diverse in color and extraordinarily bright among shield-headed vipers. Red hues prevail in the color pattern. Newborns are similarly bright in color, primarily red brown, unlike the gray young of *V. dinniki*. The typical intensive red color appears in *V. kaznakowi* after they have shed twice. Complete melanists are frequent in populations. Often the black

dorsal stripe merges with lateral stripes so that either red or yellow spots arranged in two rows along the dorsum remain. The dorsal stripe can be either zig-zag shaped or in the shape of an even broad line. Ventrums are black. Head pattern of adult specimens normally blends with the dorsal stripe. In immature specimens, the head pattern may be separated from the dorsal stripe by a light interval that disappears after maturation.

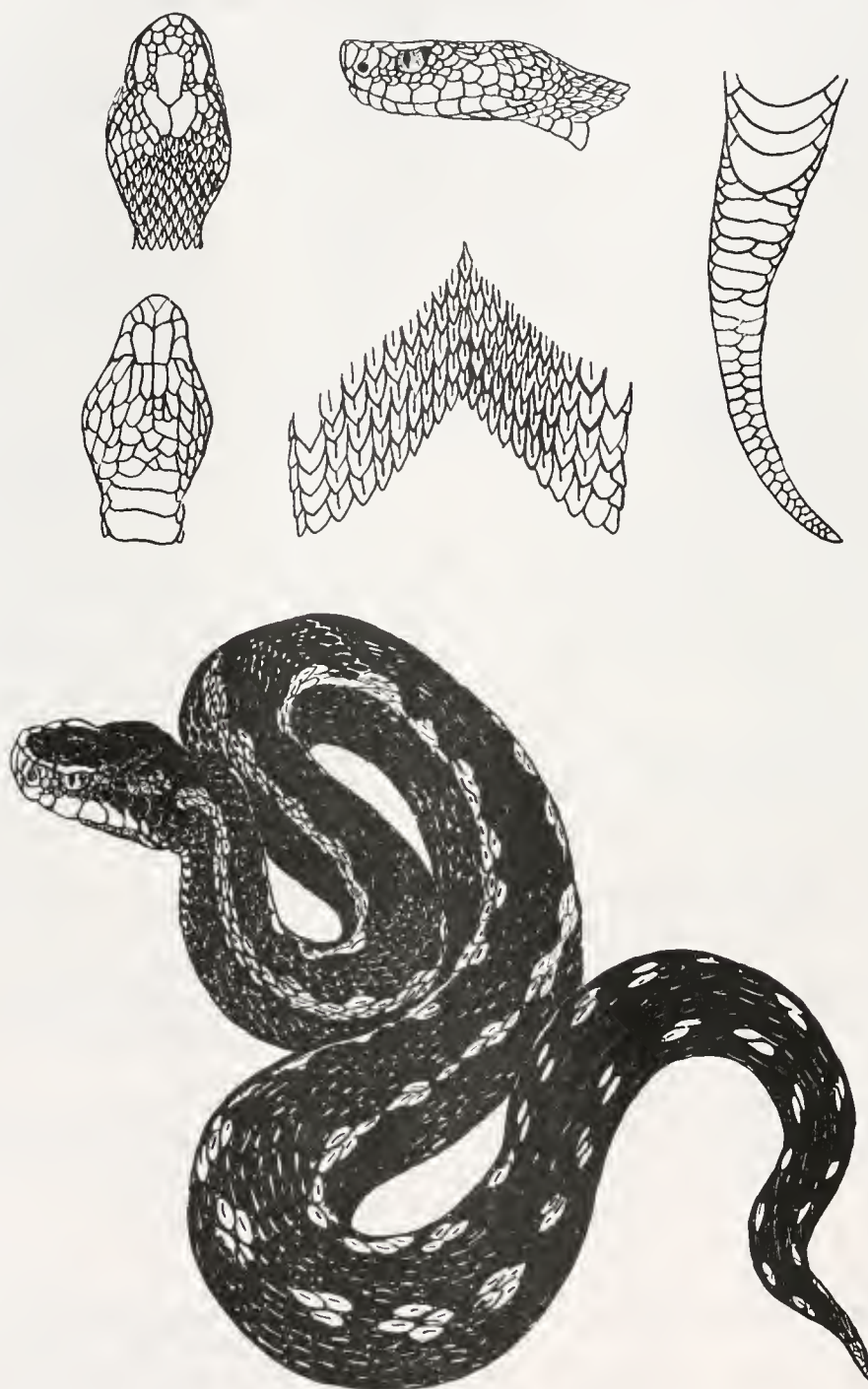


FIG. 4. *Vipera kaznakowi* (ZIN 11529) from the isolated forest of Babuk-Aul.

PLATE 1. *Vipera kaznakowi* (ZIN 11529) from the isolated forest of Babuk-Aul.

PLATE 2. One pattern variation of *Vipera dinniki* from Krasnaya Polyana (ZIN 12153), a male.

PLATE 3. *Vipera ursini eriwanensis* from the valley of Kassach, the foothills of the Ara-Fler Mountains.



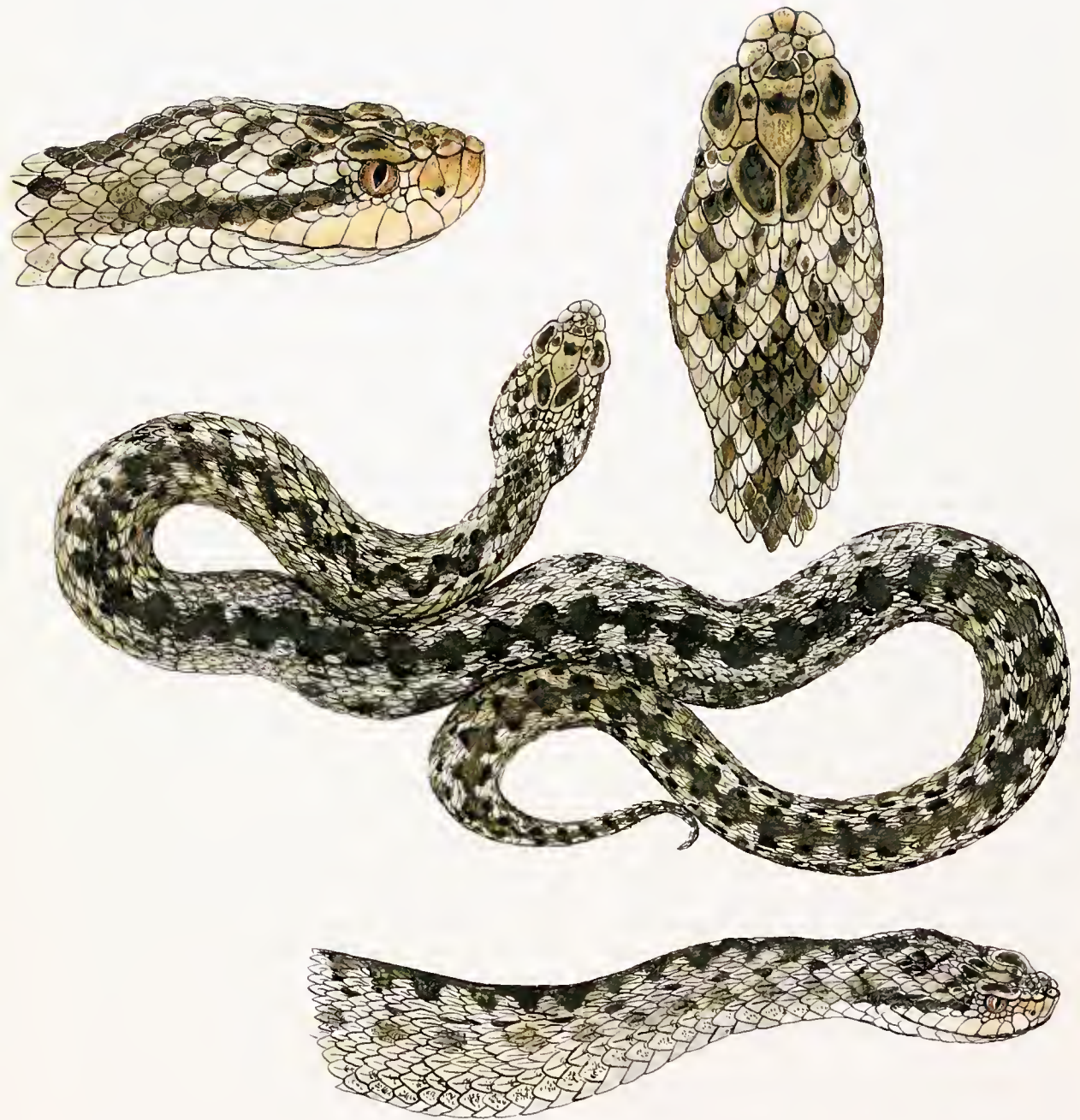
Анон 1988

Vipera kaznakowi



Vipera dinniki

Занов 1988



Vipera ursini eriwanensis

Захаров 1987

Sexual dimorphism. Maximum body length is longer in females (up to 600 mm) than in males (does not exceed 457 mm). Males have longer tails (Table 2). Accordingly, the number of ventrals is greater in females, whereas the number of subcaudals is greater in males. Males are more slender. Sexual dimorphism in coloration is feebly marked. Melanistic individuals are more frequent among females.

Age variability. *Vipera kaznakowi* are born with the typical adult color and pattern. However, in newborns these characters are less pronounced than in adults. Newborn snakes may be either pinkish or reddish. According to our observations on birth and development of snakes from the Sochi-Khosta populations, the coloration becomes stronger with each subsequent shedding. Maximal color intensity is achieved by the season after the first hibernation.

Melanistic specimens are born with the typical species pattern, but their coloration is darker. The coloration becomes darker during subsequent sheddings and elements of the pattern merge.

New born litters are homogeneously colored. On maturing, the coloration becomes diverse. Phenotypic polymorphism in mature vipers of a litter is great. Either partial or nearly complete melanism is observed in all vipers from this population. This is typical for a number of other animals from humid subtropic areas adjacent to the Black Sea coast (Bartenev and Reznikova 1935). Specimens showing maximal melanism always preserve elements of orange and red on the throat scales and chin shields, the rostral, upper labials and subcaudals. Melanistic specimens of *V. dinniki* can have completely black coloration by maturity.

Geographic range and ecology. The species ranges along the Black Sea coast from the town of Khopa, Turkey and Suramsky Pass in the east, then throughout Kolchida (Colchis) up to Mikhailovsky Pass in the west. It is then found up to the

northern slope of the Main Caucasus Ridge. Here *Vipera kaznakowi* occurs along the foothills from the settlement of Ubinskaya in the west to the town of Maikop, USSR in the north and the mouth of the Urushten River in the east (Fig. 1 from Vedmederja et. al. 1986). The species generally occurs up to an elevation of 800 m. Along the river valleys of the Black Sea coast, it may occur up to an elevation of 1000 m or even higher.

Vipera kaznakowi is a forest dwelling species. It occurs on montane wooded slopes, in the bottoms of humid canyons, and in meadows adjacent to forests. It is recorded in *Quercetum azaleorum* and *Quercetum coggygriosecornosum* oak groves, in mixed subtropic forests with evergreen subforests of *Quercus hartwissiana*, *Quercus iberica*, *Alnus barbata*, *Fagus orientalis*, *Taxus baccata*, *Laurocerasus officinalis*, *Buxux colchicus*, *Castanetum colchicum*, *Fagetum nudum*, *Salictum fontenale*, and *Alnetum struthiopteridorsum*. In addition, this species is found in polydominant forests in river terraces and large overgrown outcroppings. At the upper limits of its elevational range, the species reaches coniferous forests. It is recorded within the ecotone of *Fageto-Abieta athyridosa-maxtoherbosa*, but the viper never penetrates deep into coniferous forests. *Vipera kaznakowi* is also present within transformed areas such as meadows formed after forests are cut, fruit orchards, kitchen gardens, vineyards, and dilapidated parks (Red Data Book of the USSR 1978, 1984). As a rule, vipers occur within sites where the density of lizards is high.

Typical biotypes are as follows: small meadows and other illuminated spots in forests with an exposure providing high solar radiation in conditions of humid subtropical climate of the Black Sea coast of the Caucasus. The sites are located in the vicinity of standing water, where rocks exit that are suitable for hibernation. The climate of the Caucasus coast is greatly dependent on topographic conditions of the area that forms a narrow line between the Caucasus Ridge and the Black Sea. It is

situated from northwest to southeast along the coast. The wall of the Ridge starts from Anapa. Near Novorossiisk it reaches an elevation of up to 600 m. Near Tuapse, the wall exceeds 1000 m above sea level. At the latitude of Sochi, it is 3000 m high. The Great Caucasus Ridge presents a barrier for cold northeastern winds. This barrier separates the warm humid coast from the comparatively cold continental Prekuban area (Korostelyov 1933). In the east the Adzharo-Imeretinsky Ridge separates the humid subtropical Kolchida (Colchis) from the arid regions of the Eastern Precaucasia. The climatic zone of the Black Sea coast of the Caucasus appears to be extremely favorable for *Vipera kaznakowi*. The northwestern most localities for this species (Mikhailovsky Pass and Stanitsa Ubinskaya) coincide with Pontic and northwestern floristic regions. In relief, climate, and vegetation the northwestern region is a continuation of the southern coast of the Crimea.

The Pontic region is marked by 1) subtropical vegetation in the foothills, 2) great temperature stability, and 3) high humidity (Korostelyov 1933). The limited dispersal of the species along the northern slope of the Big Caucasus is in the region of the "Kolchidian (Colchis) Gates." Due to the lowering of the western portion of the Main Caucasus Ridge, interchange of flora and fauna of Kolchida (Colchis) and the Prekuban area occurred in the past and presently occurs. Warm humid air from the Black Sea breaks through in this part of the Ridge. On the northern slope of the Big Caucasus, it creates a small refugium on a Kolchidian (Colchis) type associated with *Castanea satyra*, *Buxus colchicus*, *Ostrya carpinifolia*, *Corylus colurna*, and others (Galushko 1974; Kharadze 1974; Kholyavko et al. 1978). Of the herpetofauna of Kolchida *Bufo verucossum*, *Triturus vittatus ophryticus*, *Pelodytes caucasicus*, and *Lacerta derjugini* occur along with *V. kaznakowi*. Along the entire area of the Black Sea coast of the Caucasus, the viper is rare. In a number of spots it has disappeared. In some situations, only single specimens of *V. kaznakowi* might be encountered.

The highest density of *Vipera kaznakowi* that have been observed are in rocky outcroppings within the forest belt in the mountains of the Caucasus Reserve. In beech forests along a road in the valley of the Achipse River, we have recorded three specimens per kilometer of road. Single specimens have been recorded in the vicinity of Khosta, Babuk-Aul, Guzeripl, and Kisha Kordons. The density of the viper is also low in the southern habitats in Adzharia and Lazistan, Georgia (Basoglu 1947; Vedmederja 1977; Basoglu and Baran 1977).

Anthropogenic factors are responsible for declining numbers and populations of *Vipera kaznakowi*. There are pressures due to recreational use of health resorts along the Black Sea coast, ploughing of sites near the foothills, and to a smaller extent, hay-mowing (Red Data Book of the USSR 1978, 1984). Within some resort areas *V. kaznakowi* is completely extinct.

Diet. *Vipera kaznakowi* feeds on various animals. Different populations show specific feeding patterns with regard to prey available. According to data recorded in captivity, individual preference is observed. When stimulated to regurgitate, the following food species were recorded in the field: *Apodemus sylvaticus*, a forest mouse, *A. agrarius*, a field mouse, *Microtus majori*, a juvenile specimen, *M. gud*, *Sorex raddei*, *Lacerta saxicola*, *L. derjugini*, *L. praticola* and *L. agilis*. In the collection of the Zoological Museum of the Moscow State University a viper specimen from Bebyssyry Lake is preserved. In its stomach a juvenile grass snake (*Natrix natrix*) was found. Immature individuals feed on juvenile lizards of the above mentioned species, and to a lesser extent, on Orthoptera.

In captivity adult vipers readily take any small rodents, fledgling sparrows, lizards, and pieces of chicken. Young vipers usually start on small lizards and crickets (*Grillus bimaculatus* and *Achaeta domestica*). After some months they usually take newborn mice. After the viper's bite a prey normally dies in 5-7

minutes. The snake never persecutes its prey. It finds the prey some time later using its olfactory organs. Swallowing ranges from one minute to 3.5 hours depending on prey size and the state of a snake. Complete digestion in the wild takes up to five days. In captivity digestion may take 30 to 40 hours at stable temperature. Optimal day temperature is 26-30°C, and night temperature 18°C during activity period.

Shedding. Mature vipers normally shed 2 to 3 times during the activity period. General shedding is observed in June. New born vipers shed in the first hours after birth. Before entering hibernation, they shed again.

Reproduction. Mating is recorded from late March to April. Birth occurs in late August. Females give birth to 3 to 5 young. The observed time of birth lasts for about two hours with intervals of 20 to 40 minutes (Zinyakova and Trofimov 1977). In captivity, the majority of females give birth at night, between 2400 and 0600 hrs. Some individuals are born in transparent capsules, which the neonates leave in the first minutes after birth. Females reproduce annually. Gravid females continue to take food right up to birth.

Development of young. Neonate *Vipera kaznakowi* have a mean body length of 144.75 mm, tail length of 14.0 mm. Mean body weight is 4.1 g (n=8). After first shedding on the second day after birth, newborns start actively feeding on insects or small lizards. After birth the activity period is 1.5 to 2.5 months, whereas newborns of *V. dinniki* never take food and almost immediately enter hibernation, during which snakes increase in length from 10 to 20 mm. *Vipera kaznakowi* lose 0.3 g of initial weight during the first month after birth. In the second month they restore their initial weight and then increase it approximately 1 g before entering hibernation. One year old specimens have a body length of 200 mm and a tail length of 24 mm. Vipers reach sexual maturity by the third year at a SVL of 350-400 mm.

Territoriality. Like other vipers, *Vipera kaznakowi* is conservative in territory use. The same individuals can be encountered in the same places during different seasons. *Vipera kaznakowi* utilizes considerably larger individual ranges than *V. dinniki*.

Seasonal and daily activity. Along the Black Sea coast of the Caucasus, *Vipera kaznakowi* emerge after hibernation in March at an altitude of 600 to 800 m. On the northern slope of the Big Caucasus the vipers appear in the second half of April to early May when the mean day temperature is 13° to 16°C. In the foothills the vipers enter hibernation at the beginning of November at an altitude of up to 600 m. In the upper elevational limits of its range *V. kaznakowi* hibernate in late September to early October. New born vipers are more active than those of other age groups.

Two sharply marked peaks of daily activity can be observed in *Vipera kaznakowi*. In the morning the period of daily activity ranges from 0730 to 1130 hrs, and in the evening from 1630 to 1830 hrs. At those times the soil temperature does not exceed 30-32°C in the sites inhabited by *V. kaznakowi*.

Sympatric species. Along with *Vipera kaznakowi* the following species of reptiles occur: *Lacerta derjugini*, *L. saxicola*, *L. praticola*, *L. agilis*, *Anguis fragilis*, *Pseudopus apodus*, *Coluber najadum*, *C. jugularis*, *Elaphe longissima*, *Natrix natrix*, *N. tessellata*, and *Coronella austriaca*. Narrow sympatric areas appear with *Testudo graeca*, *Lacerta trilineata*, *L. caucasica*, *L. rudis*, *L. parvula*, *L. mixta*, *Elaphe hohenackeri*, *Vipera ursini*, and *V. dinniki*.

Vipera dinniki Nikolsky, 1913
(Fig. 5, 6, 7, 12, 14ab, 16, Plate 2)

Species description in chronology

Vipera berus - Boettger in Radde, 1899:286; Nikolsky, 1905:304 (ad Caucasus).

Pelias cherssea - Menetries, 1832:73 (part).

Vipera xanthina - Dinnik, 1902:34.

Vipera renardi - Silantyer, 1903, 30:37 (part).

Vipera berus dinniki Nikolsky, 1913:176-179.

Coluber berus dinniki - Nikolsky, 1916:240-244.

Vipera tigrina Tzarevsky, 1916:32-37.

Vipera ursini renardi - Kramer, 1961:715.

Vipera ursini kaznakowi - Knoepfler and Sochurek, 1955:185-188.

Vipera kaznakowi - Terentyev and Chernov, 1949:270-271 (map 5); Bannikov et al., 1977:323-324 (map 133, colored plate 31,4).

Vipera kaznakowi dinniki - Vedmederja, 1984:8.

Vipera kaznakowi orientalis - Vedmederja, 1984:9, nomen nudum.

The English common name is Dinnik's Viper or the Caucasus Subalpine Viper.

Lectotype: No. 26044, an adult female collected by N. Y. Dinnik (Fig. 5) from the upper reaches of the Malaya (Small) Laba River, Northern Caucasus and Svanetia, Georgia (Fig. 2: B, B'). The specimen is preserved at the Museum of Natural History, Kharkov State University, Ukraine.

Diagnosis: Total length reaches 500 to 550 mm. Dorsally the head is covered with large scales. Nostril is cut through in the center of the nasal. Upperlateral snout edge is rounded and slightly pointed. Rostral touches either one or two apical scales on upper head. Three to four scale rows with no keels are between the rostral and frontal. Head is not broad. Nuchal collar is not expressed.

Description: In males body length is not greater than 412 mm; in females it does not



FIG. 5. Lectotype of *Vipera dinniki* (The Museum of Natural History of Kharkov State University 26044).

exceed 486 mm. The ratio of body length to tail length is 5.9 to 7.4 in males; 7.8 to 13.5 in females. General coloration is not as bright as in *Vipera kaznakowi*. However, specimens with bright yellow and orange elements can be observed. Normally *V. dinniki* (Fig. 6., Plate 2) have light brown, grey, silver greyish or green greyish color which never occurs in *V. kaznakowi*. Some specimens have a dark even dorsal stripe along the center of the body. The latter substitutes for the zig-zag shaped stripe typical for the majority of plate-headed vipers. Ventrums are either dark and light spotted or light grey and dark speckled. Neonates of *V. dinniki* occasionally don't have the red color of the body typical for *V. kaznakowi*. They can be born grey brown. The head is relatively narrower than that of *V. kaznakowi*. The nuchal collar is not expressed, unlike in *V. kaznakowi*. Upper edge of snout is either rounded or slightly pointed. Head can be either protuberant or flat dorsally, but never impressed like that of *V. kaznakowi*. Body is thinner and more delicate. Comparative data on pholidosis and size characters are listed in Tables 1-4.

Remarks and variability.

Vipera dinniki greatly resembles morphologically *V. kaznakowi*, *V. ursini renardi* and *V. berus*. In size *V. dinniki* is smaller than *V. kaznakowi* and larger than *V. ursini renardi* (Table 2). The head normally is slightly protuberant, seldom flat and never as broad as that of *V.*



FIG. 6. A Female *Vipera dinniki* from the upper part of the Laba River (ZIN 17281).

kaznakowi. Hence, the nuchal collar is hardly marked. In body proportions it primarily resembles *V. berus*. Normally the parietals are shorter than the frontal. Three to four lower labials reach the lower jaw scale.

Color. Normally *Vipera dinniki* is not as brightly colored as *V. kaznakowi*. However specimens with either bright

yellow or orange elements occur. Often *V. dinniki* have greyish, silver greyish or green greyish color. This is never recorded in *V. kaznakowi*. For all shield-headed vipers a zig-zag shaped dorsal stripe is a common pattern element. In *V. dinniki* the stripe is often an even broad dark line which runs along the dorsum. This is occasionally seen in *V. kaznakowi*, where it is usually represented by a row of oblique

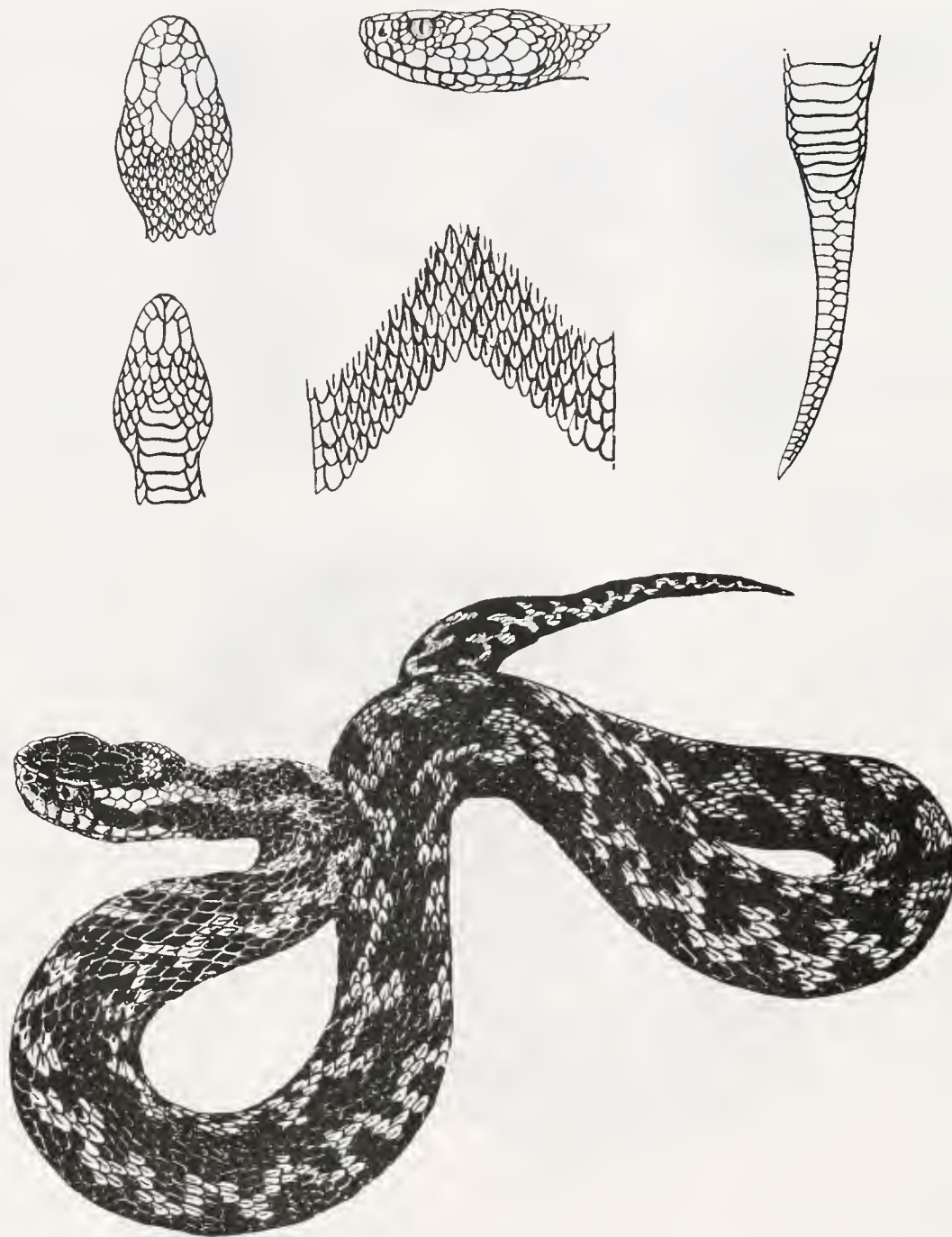


FIG. 7. A male *Vipera dinniki* from the vicinity of Krasnaya Polyana (Red Meadow), [ZIN 12153].

diametrical spots. The dorsal stripe is separated from the dark sides by lighter lateral stripes. The ventrum is either dark with light spots or light grey. The number of melanistic specimens in populations ranges from 20 to 25%. Complete melanistic individuals of *V. dinniki* do not

have a single light spot in color, unlike melanists of *V. kaznakowi*.

Sexual dimorphism. Maximum body length is greater in females (up to 486 mm), and smaller in males (up to 412 mm). Males have longer tails, characteristically

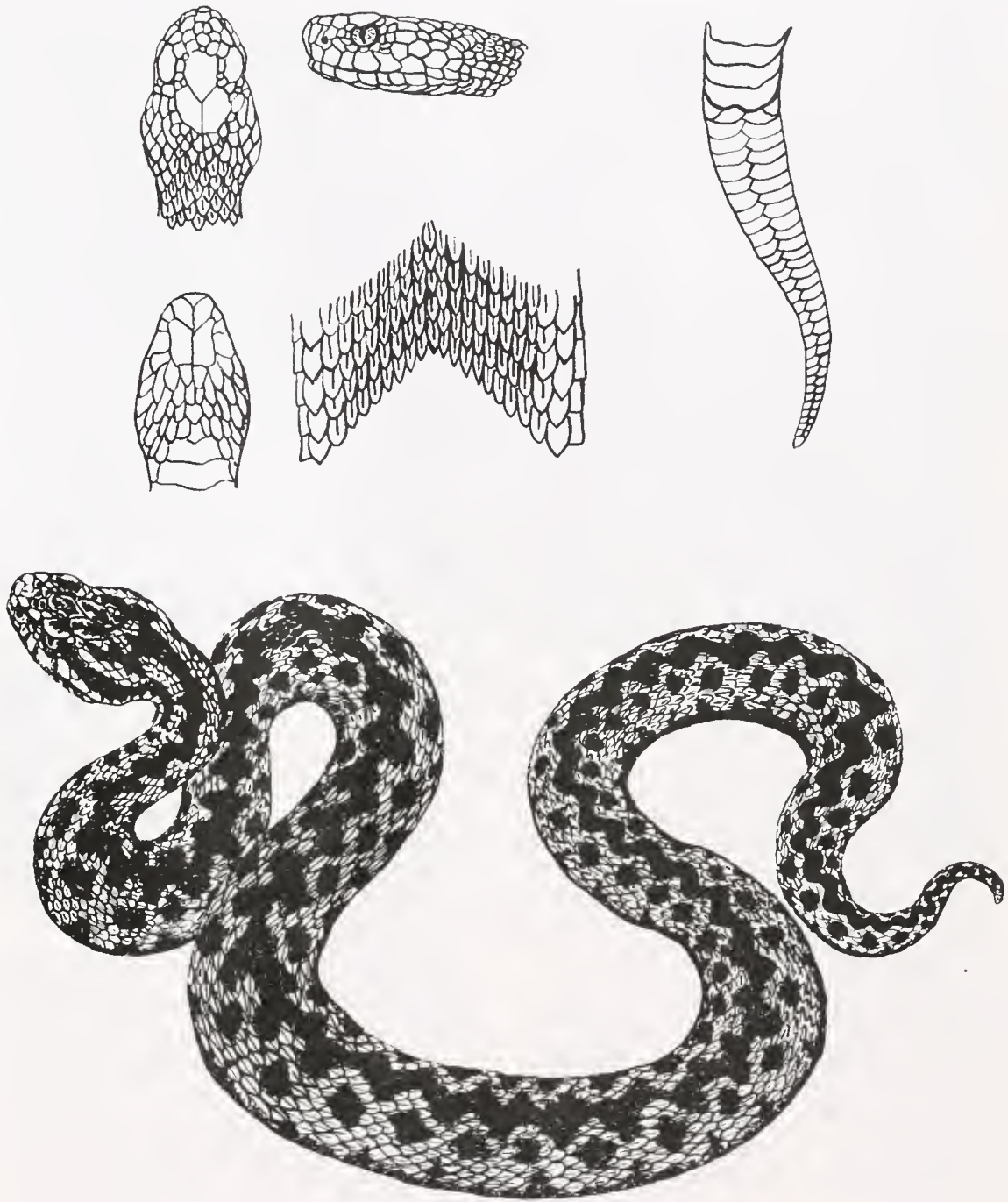


FIG. 8. A *Vipera dinniki* from Lagodekhi, an eastern population (ZIN 13769).

thicker at the tail base (Table 2). The number of ventral scales is greater in females. The number of subcaudals is greater in males. Males are more delicately built than females. Sexual dimorphism in color is hardly expressed. Coloration in males is generally brighter and more

contrasting.

Age variability. Neonate vipers are patterned like adult individuals. However, the general color is normally grey, unlike bright red neonates of *Vipera kaznakowi*. Only after the third shedding, faint

coloration typical for the species (yellow, reddish, greenish) emerges in *V. dinniki*. Color becomes stronger with each subsequent shedding. Maximum color strength is reached by maturity. Melanistic specimens are born with a specific color. They gradually darken with each shedding. By the third year, they acquire a black velvet color.

Geographical range and ecology. The species ranges from the Fisht-Oshtenovsky Mountain Range in the west up to Mount Shkhara in the east. The eastern limits of this species distribution has not been worked out and additional eastern localities are probable. The southern distributional limit runs along the dark coniferous highland ecological belt on the southern slope of the Main Caucasus and South Frontal Ridges. The northern limit goes from Mount Shkhara to the west along the crest of the Main Caucasus Ridge up to the Bolshaya (Big) Laba River head where it passes on to a northern macroslope. In the north it occurs on the Peredovoy (Frontal) Ridge and reaches the Fisht-Oshtenovsky Mountain Massive (Orlov and Tuniyev 1986). Research during 1987-1989 showed that *Vipera dinniki* occurs further to the east than previously known (Fig. 9). The problem of subspecific status of the eastern populations and their interaction with the vipers of the *V. ursini* complex will be addressed in a future paper.

The elevational distribution is generally between 1500 and 3000 m. Occasionally the viper may descend slightly lower. *Vipera dinniki* is a subalpine montane-meadow species. It tends to be restricted to the upper forest belt, subalpine and alpine meadows, rocky outcroppings and montane moraines.

Vipera dinniki can be observed in vegetation associations of *Betuletum calamagrostidosum*, *Pinetum mystillosum subalpinum*, *Fageto Betuleto-Sorbetum altherbosa-subalpinum*, also in *Aceretum trantaltherbosum subalpinum*. It is associated with rock outcrops interspaced with shrubs of *Rhodoretum caucasicus subalpinus*, subalpine highland herbs and

rock debris. It occurs widely in moraines overgrown with moss, lichens and *Thymus*. The biotype of *V. kaznakowi* is always located in the vicinity of water. Hibernation sites are also located in the immediate vicinity of summer biotypes. All types of rock outcrops are inhabited. *Vipera dinniki* can be found in limestone, slate, and crystalline outcrops.

Climatic conditions within the range of *Vipera dinniki* are much more severe than those of *V. kaznakowi*. However, the viper's distribution in severe highlands coincides with the mildest climatic places in this severe area. *Vipera dinniki* commonly occurs on slopes with a southern or southeastern exposure. For instance, on Mount Aibga, 23 km away from the sea, at an altitude in excess of 1800 m, the mean temperature in January is -0.1°C (Korostelyov 1933; Shkadova 1979). Mean temperature in July is only 13.7°C on Mount Achisko at an altitude of 1750 m (37 km away from the sea). However, great temperature drops never occur in this area, even in winter. As regards to soil freezing, minimum temperature in January is -7° to -8°C (Selyaninov 1933). Due to solar radiation on slopes with southern and southeastern exposures, the vipers manage to maintain high body temperatures during activity periods.

Vipera kaznakowi reaches the edge, but does not penetrate deep into the dark coniferous belt. *Vipera dinniki*, at its lower limits, reaches the edge but never penetrates the dark coniferous belt. Thus, the dark coniferous belt is a barrier between them. Occasionally, in spots where this belt is either absent or is fragmented, for instance along river valleys, both species occur sympatrically, forming a narrow line with intergrading characters. The valley of the Mzymta River may serve as an example of a site where the two species come in contact. The limited distribution of the species on the northern slope of the Main Caucasus Ridge might be connected with the increase of the mountain's aridity and severe climate towards the east. Xerophytization is observed from west to east in the subsequent change of beech

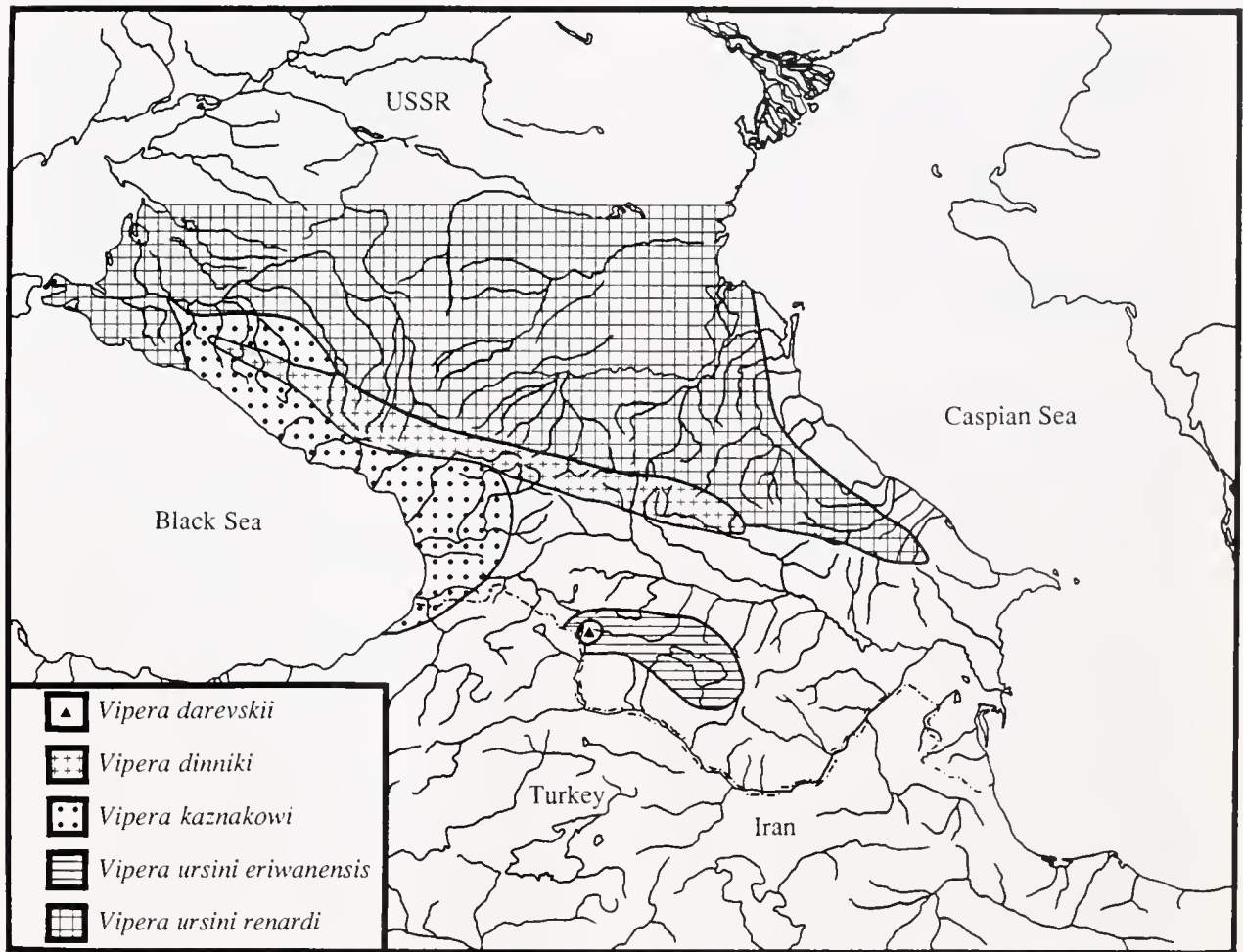


FIG. 9. Distribution map of shield-headed vipers in the Caucasus.

forests and *Abies* forests to pine forests, and further east, to steppe areas (Adamyants 1971, Kharadze 1974, Lavrenko 1980; Agakhanyants 1981). This change is noted in amphibians and reptiles. Along with *V. dinniki*, *Lacerta derjugini* and *Pelodytes caucasicus* fall out and more xeric species such as *Bufo viridis*, *Lacerta agilis*, and *Vipera ursini renardi* dominate.

Population density is different in various parts of the habitat. It is maximal on rock outcrops and moraines in the subalpine belt of the Caucasus Reserve. In July, in subalpine meadows of the Gertsen Ridge and along the valley of the Bezymyanka (Without name) River, 1700 to 1900 m, we have recorded as many as 5 to 7 vipers per 1 km of a route. At the same time, on an

area of 500 m², we have recorded up to 6 specimens. This is at an elevation of 1800 m on the Aishkha Ridge in a subalpine meadow of *Aceretum trantaltherbosum subalpinum*. In late June to early July along the Moloshnaya (Milk) and Sumasshedshya (Crazy) rivers of the Mzymta River basin, up to 4 specimens per 100 to 500 m of a route were recorded. In August, on a bank of the high altitude Kardavych Lake, we recorded up to 8 specimens per 300 m of a route. On the Aspidny Ridge, 2000 m above sea level, we recorded 5 to 6 specimens per 300 to 400 m of a route.

According to Bozhansky (1979), the density in the subalpine belt is 2 to 6 specimens per hectare. Occasionally, seasonal accumulations of up to 30-40

individuals per hectare are possible. In other regions the population densities are much lower. Degradation of localities is due to intensive cattle grazing in subalpine meadows. Overall numbers of both *V. kaznakowi* and *V. dinniki* are estimated at some dozens of thousands (Bannikov and Makeyev 1976). Apparently the figure may primarily concern *V. dinniki* as the number of *V. kaznakowi* is rather small.

Diet. Adult *Vipera dinniki* eat fewer types of food items than *V. kaznakowi*. For instance, in the highlands there are viper populations that prey either on lizards or on small mammals as no other food items are available. When field collected vipers were stimulated to regurgitate, the following prey were observed: *Apodemus sylvaticus*, *Microtus majori*, *Sicista caucasica*, fledglings of ground nesting birds such as *Anthus spinoletta*, and *Lacerta caucasica*. Immature specimens feed on Orthoptera and small lizards. In captivity *V. dinniki* takes similar food items as *V. kaznakowi*. It is often observed that a bitten mouse or a field-vole makes a few desperate leaps, falls into a deep crack between rocks and dies there. The viper skillfully catches its prey between its teeth, drags it out onto a level spot, then drops it, examines it from all sides and having found the prey's head, swallows it. This behavior is typical for other rock dwelling vipers from the Caucasus, such as *V. raddei*, and *V. ammodytes*.

Shedding. Overall, shedding is observed in June and in late August to early September. Neonate vipers shed during the first hours after birth. Some days later they enter hibernation.

Reproduction. Copulation occurs in late April to May (Bozhansky 1984). Birth of neonates on the northern slope of the Main Caucasus Ridge occurs in August. On the southern slope it occurs throughout September. Bozhansky (1983) found two groups of specimens during the summer. One group containing males and females which do not reproduce that year, and the other group containing gravid females. Bozhansky suggests that in montane

conditions, female *Vipera dinniki* have a reproductive cycle of many years.

Development of the young. In late July to early August viper embryos reach 70 mm in length (Orlova 1973). Mean body length of the neonates is 131.0 mm, tail length is 14.8 mm, mean weight is 3.1 g (N=28). In the highlands almost right after birth the vipers enter hibernation. Unlike newly born *Vipera kaznakowi*, they do not feed until the next season. By the third year the vipers become mature.

Territoriality. Gravid females tend to move on small areas ranging from 1-4 to 51 m². Their individual places to a great extent (up to 98%) overlap. Within their sites the vipers actively utilize only 2 or 3 places where they may be encountered at different times and under various weather conditions. During the morning the vipers can be found in places with a western exposure. Normally, this place is on a rock surface shaded by a bush. The vipers utilize direct sun for a short time, leaving a part of the body under the sun and a part under a half shaded area. From 1100-1200 the vipers retreat to burrows and normally appear after 1500 hours. In gloomy weather they lie flat on a rock during the entire period of activity. This increases the surface of the body contiguity with the rock. On rare hot days, after midday the vipers never reappear on the surface. Males and non-reproducing females emerge much more seldom, normally after they have taken food. Bozhansky (1984) observed some specimens using the same territories for three seasons.

Insolation is of great importance in the viper's life. Gravid females take food rarely and two months before giving birth, they stop eating. Territory utilization is entirely dependent on optimal insolation patterns. Absence of aggressiveness allows all adult females in a territorial group to utilize the warmest microhabitats (Bozhansky 1983, 1984). These data were collected by Bozhansky during three summers at an elevation of 2000 m along the border between the forest and subalpine belts on Aishkha Ridge, the right ridge of

the Mzymta River valley, the western Caucasus. It is amazing that *Vipera kaznakowi* from the low altitudes of the coast have considerably larger individual sites. The females do not have a multi-year cycle and never stop taking food while gravid. The adaptations in the highland *V. dinniki* are very important in relatively low temperatures, rainy periods, and when it suddenly becomes cold.

Seasonal dynamics in populations.

Biological monitoring in highland populations from the Caucasus Reserve testify to their climax state (the collections of the Zoological Museum of the Moscow State University and the Zoological Institute, the USSR Academy of Sciences were adopted as a zero counting point). Seasonal dynamics within climax populations is monotypical. At the beginning of spring, males emerge first. Then the percentage of female occurrences gradually increases. By early-mid June the sex ratio is 1:1. In mid-late summer males are seen on the surface less frequently than females. During the period of pre-hibernation at the end of summer, males become more common again. From late August to mid September, 80% of the snakes observed are gravid females and new born individuals. The later can be observed on the surface even when adults have entered hibernation. During this period, the location of new born individuals does not necessarily correlate with rock outcrops which are used as winter shelters. The newborn snakes migrate much more than adult snakes.

Seasonal and daily activity. In the spring vipers emerge from mid April to May when mean day temperature on the surface reaches 11°C. Seasonal activity is dependent on weather conditions. In the highlands of the Caucasus Reserve the first snow usually falls in the second half of September and snow is present until May. Snow cover is 7-8 m thick. Hence, *Vipera dinniki* inhabiting the subalpine belt enter hibernation in the second half of September. At elevations of 1800 to 2400 m morning activity is hardly expressed, whereas evening activity is

shifted from 1700 to 2000 hrs. In gloomy weather snakes are active throughout daylight at temperatures higher than 10°C. At 8°C vipers are not seen on the surface. Gravid females are seen on the surface even in drizzling rain. Even if the temperature is 10°C, body temperature in vipers is 30°C, and cloacal temperature is 26-28°C due to accumulation of warmth from solar radiation. This is an important thermal adaptation of a number of highland reptiles.

Sympatric species. Throughout nearly the entire range *Vipera dinniki* is sympatric with *Lacerta caucasica*, *L. saxicola*, *Anguis fragilis*, and *Coronella austriaca*.

Vipera darevskii Vedmederja, Orlov,
and Tuniyev, 1986
(Fig. 10, 11, 12, 13)

Chronology of species description

Vipera kaznakowi dinniki - Darevsky, 1956:128.

Vipera kaznakowi darevskii - Vedmederja, 1984:8, *nomen nudum*.

The English common name is Darevsky's Viper.

Holotype: ZIN 19934, an adult female from Legli Mountain, the Mokrye (Wet) Mountains, Gukasynsky region, Armenia. The specimen was collected in June, 1980 by I. S. Darevsky. The specimen is preserved at the Zoological Institute, the USSR Academy of Sciences, Leningrad (Fig. 10).

Paratypes: ZIN 16546 a and b. The specimens were collected May 28, 1954; ZIN 17545, the specimen was collected August 6, 1955; ZIN 19935, the specimen was collected June, 1980 by I. S. Darevsky (Fig. 11).

Holotype description: Body length is 421 mm, head included. Tail length is 46 mm. A female. Head is slightly impressed dorsally. Lateral snout edges are slightly pointed. Anterior edge of snout is slightly rounded. Rostral is narrow. Frontal is

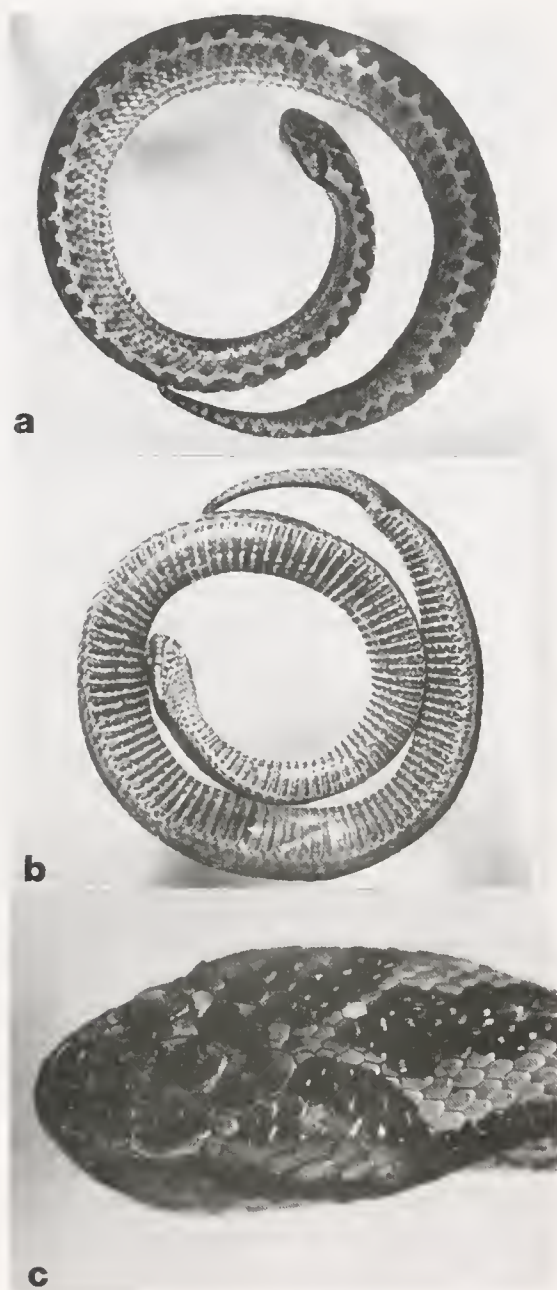


FIG. 10. Holotype of *Vipera darevskii* (ZIN 19934). a. dorsal view, b. ventral view, c. head.

narrow. Its length is equivalent to 1.66 times its width. Parietals are slightly longer than the frontal. The frontal is separated from supraoculars, which protrude over lateral edge of the snout, by a row of three scales. Prefrontal is triangular, three times shorter than the frontal, and is separated from the rostral by 2 scale rows. Nostril is cut through in the lower part of the nasal.

The latter is separated from the rostral by a broad scale. Upper labials and lower labials are both 9 to the right and 8 to the left. There are 5 rows of throat scales. Around the center of the body there are 21 scale rows with strongly expressed keels, except for two scale rows on both sides adjacent to the ventrals, which are smooth. The number of ventrals is 138. There are 25 pairs of subcaudals.

The color is yellowish grey. A zig-zag shaped brown stripe runs along the dorsum. At the center of the body its width is nearly 8 mm. A row of hardly conspicuous spots is present laterally. The spots merge into a light brown stripe. Dorsally, the head has light yellowish spots along the edges of the frontal, parietals and lower oculars with yellowish temporals. Ventrals are blackish marked by light contours of ventrals (Fig. 10).

Paratypes: Morphological characters of 8 paratypes are listed in the tables 1-4. General color resembles that of the holotype, except for 2 specimens. In the latter the dorsal stripe is interrupted in the anterior part of the body (Fig. 11).

Diagnosis: This viper is not large. SVL reaches 460 to 489 mm. Head is slightly impressed dorsally, covered by big scales. Lateral edges of snout are slightly pointed. Anterior snout edge is rounded. Nostril is cut through in lower part of the nasal. Head is narrow, hardly separated from body.

Remarks and variability.

Morphologically, *Vipera darevskii* occupies an intermediate position between *V. kaznakowi* and *V. ursini eriwanensis*. To be more precise, morphologically *V. darevskii* occupies a middle position between the two species of the "*Vipera kaznakowi*" complex (*V. kaznakowi* and *V. dinniki*), on the one hand, and the steppe vipers from the "*V. ursini*" complex, on the other hand. This viper is considerably smaller in body size than *V. kaznakowi*. The head is narrower and the nuchal collar is less expressed. It differs

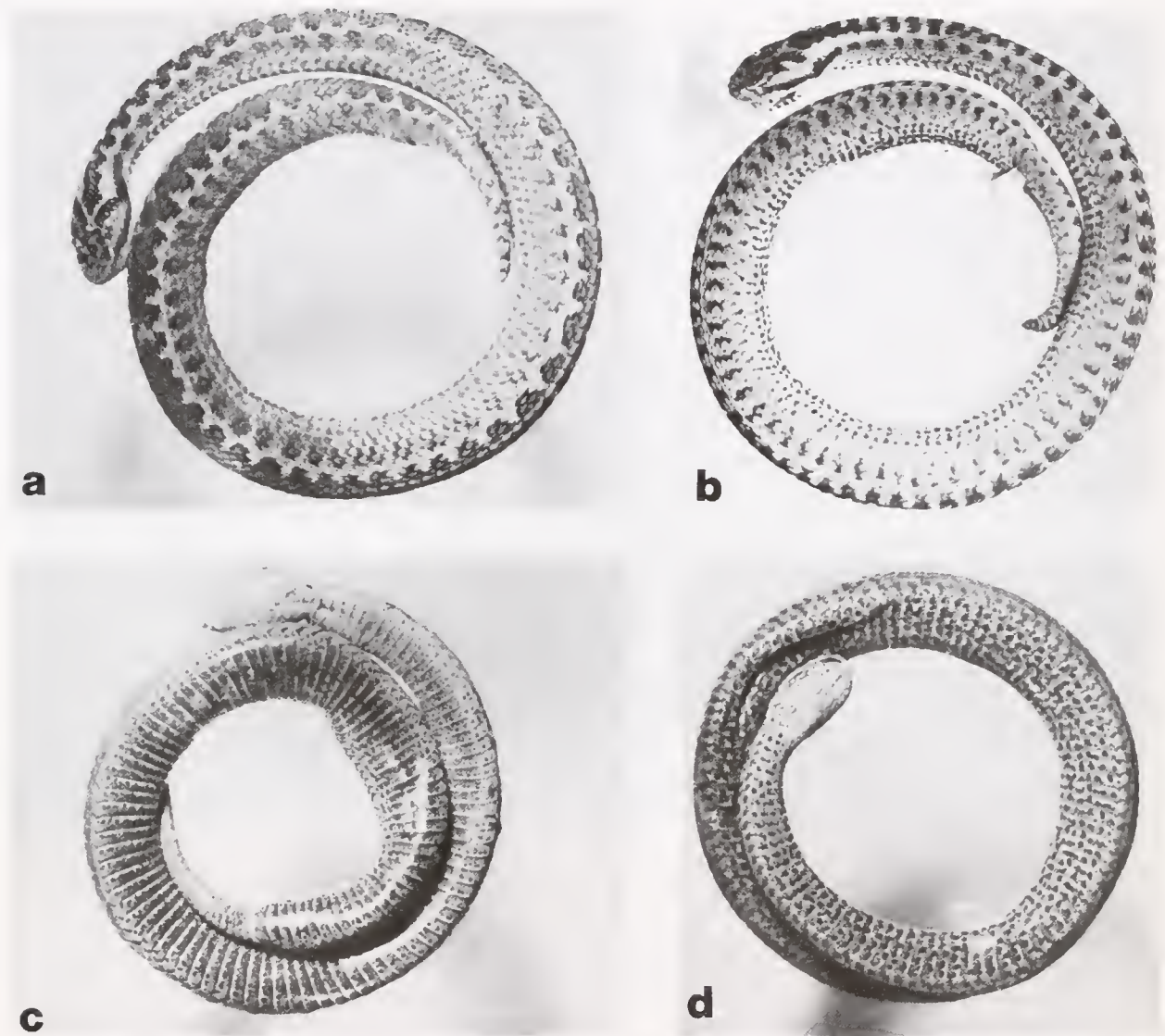


FIG. 11. The paratypes of *Vipera darevskii* (ZIN 19935). a., b. dorsal view. c., d. ventral view.

from *V. ursini eriwanensis* by greater head height and much less pointed upper anterior snout edge. Pholidosis data are listed in Tables 1-3.

Coloration is yellowish or yellowish grey, which never occurs in *Vipera ursini*. Along the dorsum a contrasting zig-zag shaped brown stripe is present. The ventrum is dark grey, speckled black and white. Of the small number of known specimens, no melanistic individuals have been found. The coloration of *V. darevskii* is evidently more stable than that of the polymorphic and motley colored *V. kaznakowi* and *V. dinniki* (Fig. 13).

Yellow-greyish hues are prevalent. The pattern is more homogeneous. The neck transition is hardly expressed, like in *V. dinniki*. It differs from *V. ursini eriwanensis* by 1) a relatively high head, 2) yellowish general coloration, 3) clear contrasted pattern, and 4) special pholidosis.

Sexual dimorphism. Maximum body size is greater in females than males (Table 2). Males have longer tails. Number of ventral scales is greater in females (Fig. 14). Number of subcaudal scales is greater in males. Sexual dimorphism in color is not recorded.



FIG. 12. *Vipera darevskii* in the field.

Age variability. Newly born vipers are uniquely colored.

Geographic range and ecology. The species range shows relict characters. It covers the southeast part of the submeridian Dzhavakhetzky Ridge within the territory of Armenia (here this ridge has the name Mokrye (Wet) Mountains) and evidently adjacent regions of Georgia (Fig. 1: 9). Vertical distribution lies within a narrow interval at elevations from 2600 (rarely 2500) to 3000 m on Mount Legli, Georgia. It is a montane meadow subalpine species inhabiting detritus slopes with great amounts of big black outcrops of volcanic rocks at angles of 35°-45° (Darevsky pers. comm.). At recorded elevations, according to Tumadzhyanov (1980), subalpine meadows (so called Transcaucasian oats outcrops) are widely represented. It is a leading formation on steep slopes with all exposures which form the first stages of

invasion of bare rock outcrops. Characteristic components of these meadows are as follows: *Festuca woronowii*, *F. ovina*, *Bromopsis variegata*, *B. villosula*, and *Carex tristis*. Lower along the slopes at elevations from 2300 to 2400 m the formations of transition montane-meadow steppe are replaced by montane *Festuca valesidea* and *Stipa* (feather grass). From elevations of 2200 m down to 1000 m *Festuca valesiaca* steppes occur (Lavrenko 1980). Here in the montane-steppe highland ecological belt, *Vipera ursini eriwanensis* occurs in contact with *V. darevskii* in the transition zone of the meadow steppes.

The numbers of *Vipera darevskii* are not great. To date it is known only from the type locality cited as "Mount Legli", where it occurs within a narrow band in subalpine meadows. The species biology is nearly unknown.

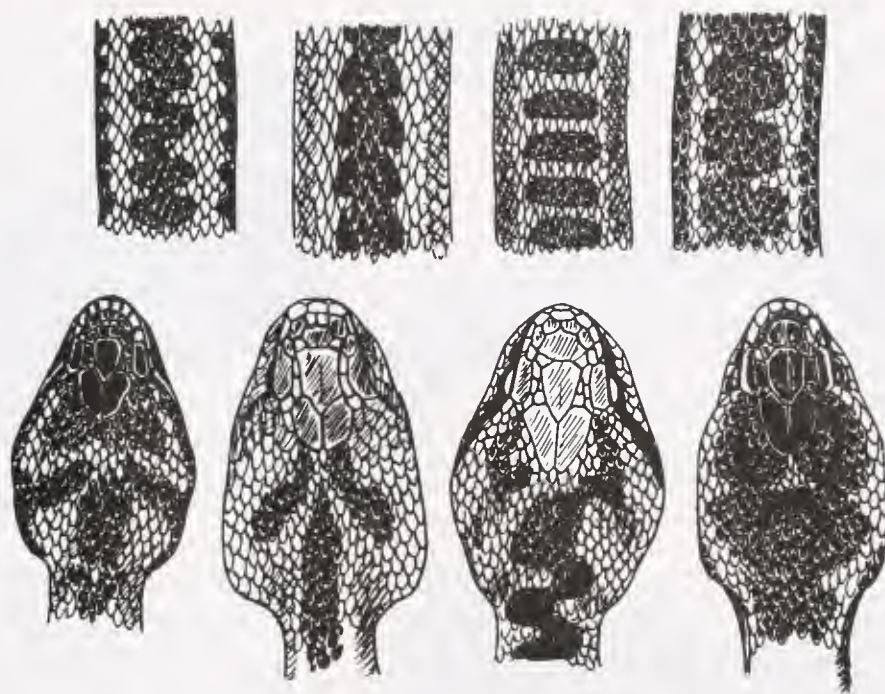


FIG. 13. Polymorphism in *Vipera dinniki* from the population that occurs in the valley of the upper part of the Mzymta River.

Discussion

Phylogeny and the history of present viper distributions in the Vipera kaznakowi complex in the Caucasus Isthmus.

The head of the vipers assigned to *Vipera berus*, *V. ursini*, and the *V. kaznakowi* complex (Fig. 15) is covered with rectangular scales (the rostral, nasals, nasal-rostrals, upper oculars, parietals, and the frontal), unlike in *V. lebetina*, *V. xanthina*, *V. raddei*, and *V. persica*. In the latter species, small scales on the upper head are typical.

Marx and Rabb (1965) consider these characters important in the assessment of phylogenetic relationships of the vipers. On the basis of body vertebrae close relationships and isolation of *Vipera berus*, *V. ursini* and *V. kaznakowi* within the genus *Vipera* have been proposed (Chkhikvadze and Zerova 1983). They restore the prior generic name of *Pelias* to the vipers. Reuss (1935) noted the isolation of the vipers that have large

regular head plates, on the basis of skull kinesis and analysis of the head muscles. Without going into extensive detail on the taxonomic position of these vipers with large regular head scales from the Euro-Siberian group, we shall simply refer to them as shield-headed vipers. These vipers show great morphological resemblance. They share a common color pattern, behavior, and reproductive biology.

We consider *Vipera berus* and *V. kaznakowi* to be close relatives. These vipers probably diverged from a mesophilic form in the Miocene. Northern populations tend to be restricted to humid biotypes up to tundra areas, whereas for southern populations, humid subtropical forests are inhabited. In Kramer's (1961) book concerning the taxonomy of *V. ursini* and *V. kaznakowi*, in the chapter on phylogeny and history of the vipers distribution, he regards *V. berus* and *V. ursini* as a united circle of races, a *rassenkreis*. Such facts that *V. ursini renardi* was subspecifically included in *V. berus* also emphasizes close relationships of shield-headed vipers.

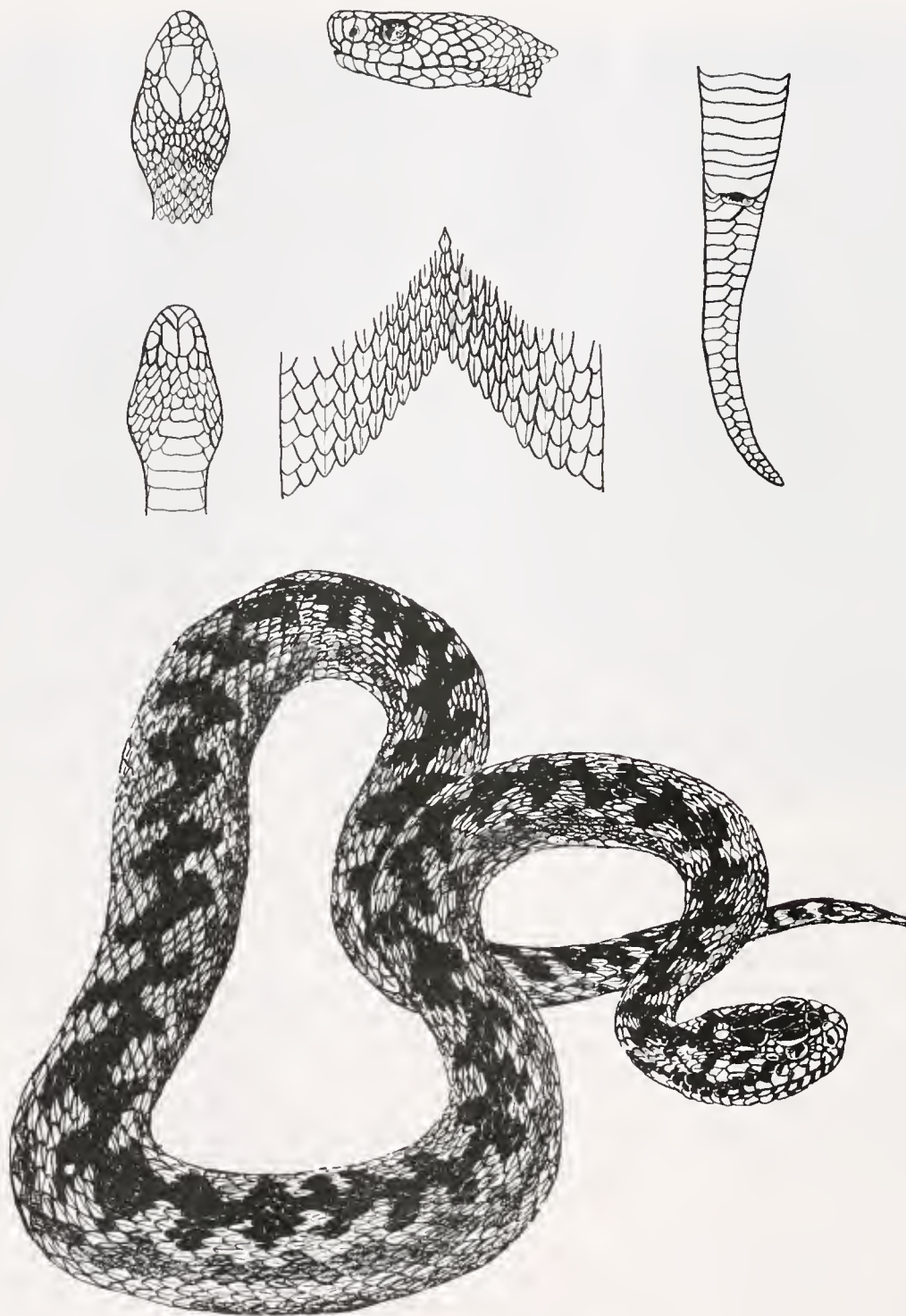


FIG. 14. A female *Vipera darevskii* from the vicinity of Gukasyansky Region, Armenia (ZIN 19934).

Basoglu (1947) recognized the following varieties within *V. berus*: *berus*, *renardi*, *ornata*. His view point was criticized and the *V. ursini renardi* was restored

(Terentyev and Chernov 1949; Mertens 1952 a, b). Kramer (1961) noted great morphological resemblance in *V. berus* and *V. kaznakowi*. He considered them

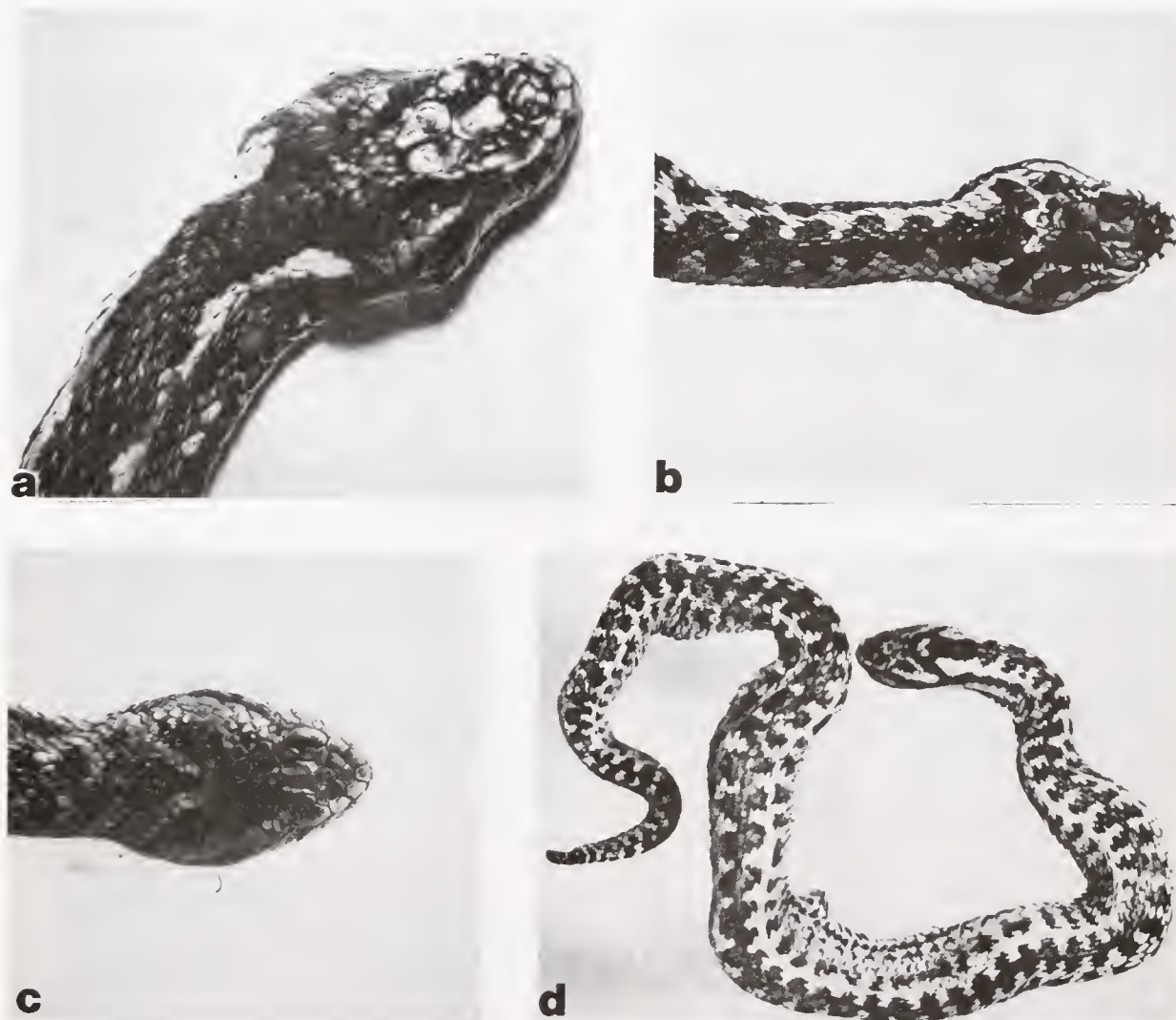


FIG. 15. The shield-headed vipers from the Caucasus. a. *Vipera kaznakowi*, b. *V. dinniki*, c. *V. ursini renardi*, d. *V. dinniki* (Lagodekhi, Georgia. ZIN 8389).

phylogenetically close species and felt that montane populations of the vipers played a big role in the formation and isolation of the forms. In his opinion, when it became cold they were forced out of the mountains onto the plains by glaciers. When the climate became warm again, they retreated into the mountains. In the mountains it was easy to choose temperature and humidity optima, whereas on the plains this was not possible. Kramer felt that in some places on the plains where refugia might be present, the climate remained more or less stable. For the vipers in the *V. ursini* complex, Kramer suggests first separation in the Miocene and Pliocene and later

independent development of the eastern and western forms. The complex formation of the climate and relief in the Caucasus coincides with regular regressions and transgressions of the sea. Breaks in links between the faunas of the Caucasus and the European platform, the Balkans and Turkey stipulate emergence and isolation of original viper forms, beginning with the Miocene and Pliocene. At this time the formation of the Caucasus as a montane country occurred (Bogachev 1938). Schwarz (1936) suggests that the viper fauna of the Mediterranean islands are Miocene relicts.

Present ranges of shield-headed vipers in

the Caucasus have precise altitudinal and ecological limits to their distributions. They are supported by natural historic events. Overlap of ranges occurs in comparatively small areas. The "*kaznakowi*" like vipers evidently invaded the Caucasus during the Miocene from the south, when the Caucasus island was connected with Middle Asian land. The southern invasion of the Caucasus in upper Miocene by different mammal species was observed by Vereschagin (1958); that of lizards from the *Podarchis-Archaeolacerta* groups was noted by Darevsky (1967). Fossils of *Vipera* have been known in Europe since the Miocene (Tatarinov 1964). Of the European Miocene fossils, *Provipera boettgeri* Kinkelin 1892, was described. Of those from lower Pliocene, *V. gedulyi* Bolkay 1913, was described by Marx and Rabb (1965). This was at about the time the Caucasus Mountains were formed (Bogachev 1938). A warm subtropical climate which stimulated rich development of mesophilic vegetation, and contributed to the formation and wide distribution of warmth and mesophilic species like *V. kaznakowi* in the Caucasus, including the Adzharo-Imeretinsky Ridge where even until the Pliocene, bay trees, rubber plants, araucarias and palms were preserved (Vereschagin 1958). Different mammal fossils: Middle Asian and Caucasus hamsters, *Mesocricetus*, *Prometheomys*, *Sorex*, and *Talpa* (Vereschagin 1958) and also those of insects: Orthoptera, Hemiptera, Blattoidea, Coleoptera (Rodendorf 1939) testify to the presence of good foodstuff for the shield-headed vipers in the Miocene.

The end of the Tertiary period was marked by a decrease in tectonics and with the emergence of a broad link between the Caucasus and the Balkans via the Crimea (Vereschagin 1958). Steppes arose in northern areas adjacent to the Black Sea coast (Pidoplichko 1954; Scherbak 1966). During this period an arid adapted "*urisini*"-like viper associated with steppe areas penetrated into western Precaucasia from the east. It might have already separated from *Vipera ursini renardi* and have become widely distributed throughout

the plains area along the northern slope in the Big Caucasus.

The middle-upper Pliocene, when the ridges of both the Big and Small Caucasus were subjected to considerable glaciation, should be considered the beginning of the initial break in the range of *Vipera kaznakowi* (Markov et al. 1965). The Kolchida (Colchis) had become a basic nucleus in *V. kaznakowi* dispersal. There, even in the epochs when it became severely cold in the Pleistocene, a relatively warm-loving vegetation of a Caucasus type was preserved (Vereschagin 1958). Along with Kolchida (Colchis) much smaller refugia were sporadically preserved along the Black Sea coast up to the town of Lazorevskoye. The same is true for the northern slope of the Main Caucasus Ridge between the Pshekha and Malaya rivers. This is supported by the present distribution of the Tertiary vegetation of the Kolchida (Colchis) type in the western Caucasus (Adamyants 1971; Kharadze 1974; Pechorin and Lozovoy 1980; Kholyavko et al. 1978; Tuniyev 1990, this volume).

It is in the narrow humid canyons with a relatively regular thermal regime that *Vipera kaznakowi* is preserved. Also, isolated populations might be preserved in midlands where the refugia with Kolchida (Colchis) vegetation are known in regions of the Fisht-Oshterovsky Massive, the Lago-Naki Plateau, and even in the Central Caucasus (Kharadze 1974; Kholyavko et al. 1978). Small refugia might also be preserved along the southern slope of the eastern Big Caucasus. Similar refugia for *Archaeolacerta* were recorded by Darevsky (1967). Most highland populations of *V. kaznakowi* undoubtedly went extinct during the glacial period. Those that were preserved in refugia have been accumulating unique characters. Data obtained by Takhtadzhian (1946) and Maruashvili (1956) reveal that in glacial epochs, mean annual temperature never dropped lower than 1.5-2.0°C, and the amount of precipitation was never less than 1500-2000 mm. These data support the proposed preservation of relictual *V.*

kaznakowi populations in the mountains.

Darevsky (1967) regards this argument as proof that due to the development of montane glaciers, a fundamental reconstruction of all animals and plants in these areas occurred from premontane and montane refugia. Lizards for example, might have been preserved in the Gagrinsky and Bzyb'sky ridges facing the sea, along with other regions. The end of the Pleistocene was marked by the development of steppe landscapes on the Zakubauskaya sloping plain along with already formed landscapes and a characteristic biological community of the present type along the Black Sea coast of the Caucasus (Vereschagin 1958). This situation contributed to a much wider dispersal of *Vipera ursini renardi* and further preservation of *V. kaznakowi*.

During the xerothermal epoch in the Holocene, intensive glacial melting and the upwards elevational shift of vegetation belts along the mountain slopes occurred throughout the area. Within a considerable area of the Caucasus, steppe landscapes became prevalent. This allowed the steppe animals, including the steppe viper, *Vipera ursini renardi*, to ascend into the mountains (Vereschagin 1958). At that time an initial contact of *V. ursini renardi* with montane relict populations of *V. kaznakowi* might have occurred in the midmountains of the Western Caucasus. This region is presently inhabited by *V. dinniki* which shows mixed morphologies of both *V. kaznakowi* and *V. ursini renardi*. The approximate ways of possible interaction and characters are shown in Fig. 16.

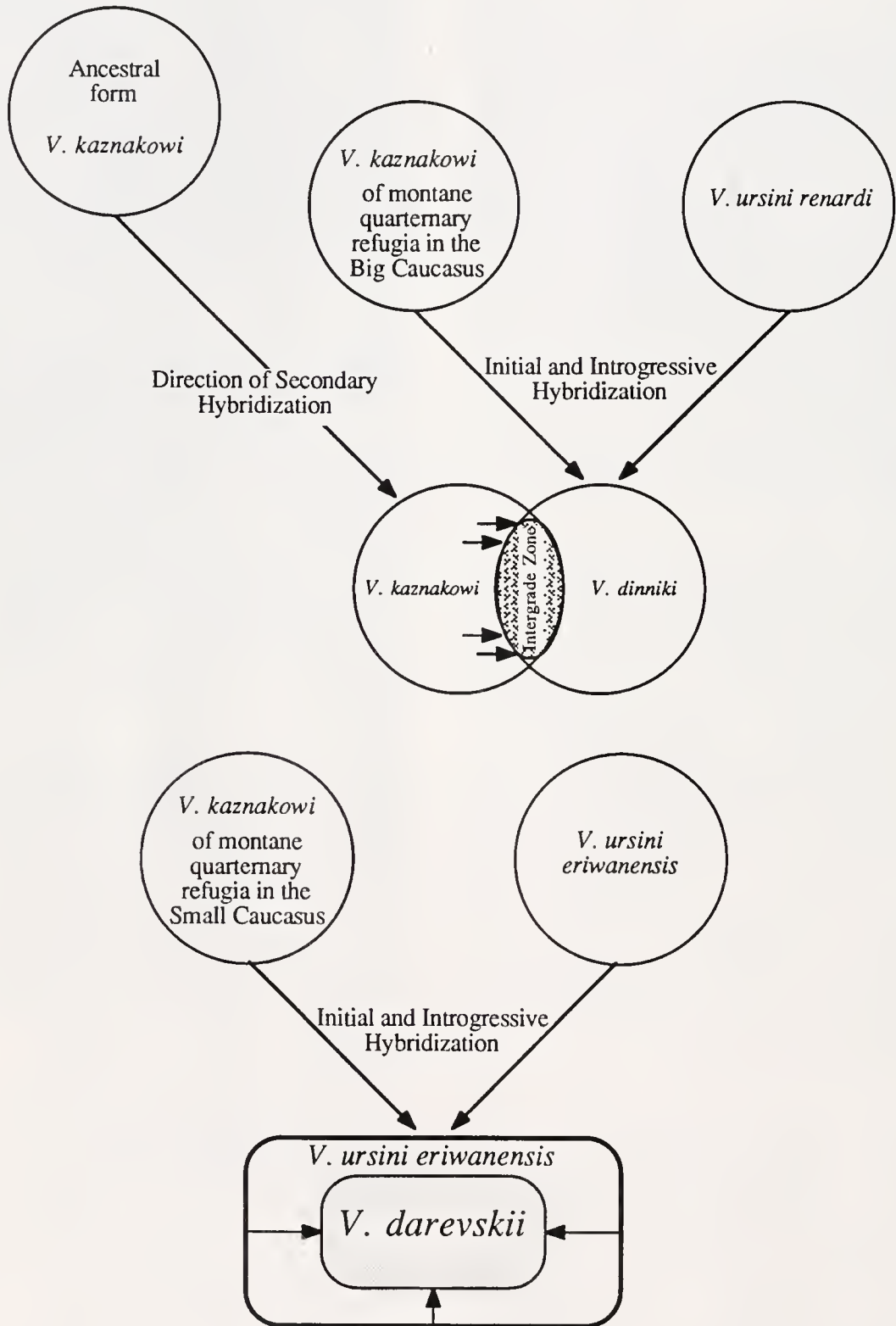
Darevsky (1967) writes about the form-building role of hybridization in the Caucasus. He observes the genesis of new forms in the lizard group *Archaeolacerta*. Hybridogenity in *Vipera dinniki* is problematic, whereas introgressing hybridization in the zones of contact between *V. kaznakowi* and *V. dinniki* is presently not doubted, age interbreedings apparently occurring in midmontane populations of *V. dinniki*. For example, in one of these populations associated with the

Mzymta River head, all the initial types of vipers can be found (Fig. 15). In premontane populations of *V. kaznakowi* we have not found specimens which have hybrid characters. Generally all premontane populations of *V. kaznakowi* show great homogeneity. In the eastern range of *V. dinniki* the species is presently disjunct geographically from the closely related *V. ursini renardi*, but rare individuals with an intermediate morphology between these species are present.

Mayr (1968), Borkin and Darevsky (1980) and Solbrig and Solbrig (1982) report on various types of hybridization. For instance, it is recorded that hybrids possessing vital capacity occur between sympatric species. Some of these hybrids are capable of recurrent crosses with one or both parental forms. The fate of both species between which hybridization occurs is partially dependent on 1) the intensity of hybridization occurring between them and 2) the level of genetic and ecological sterility of hybrids (Solbrig and Solbrig 1982).

In most cases the hybrids themselves do not have greater evolutionary significance. Rather it is the products of recurrent interbreeding between the hybrids and the parental forms, i.e. the process of introgressive hybridization, that may form new taxa; i.e. the blending of genomes of ancestral taxons, or "borrowing" of parts from other genomes by means of introgression of genes as a variant of hybridogenic species formation (Mayr 1968; Borkin and Darevsky 1980).

After the xerothermal epoch, the climate again became more humid. This fact contributed to the restoration of the former limits of the forest belt (Vereschagin 1958). Throughout the subalpine belt along the southern slope of the Main Caucasus Ridge within the area from the Central Caucasus up to the Fisht-Oshtenovsky Massive in the west, subalpine meadows and montane curved forests are widely developed (Galushko 1974; Dolukhanov 1974; Kharadze 1974; Kholyavko et al. 1978).

FIG. 16. Model of the proposed genesis of the vipers from the *Vipera kaznakowi* complex.

In the western part, this vegetation is present along the northern slope. To the east, it gradually changes to steppe (Lavrenko 1980). Definite limits of the subalpine belt in the area influenced by the warm Black Sea mark the present distributional limit of *Vipera dinniki*.

The final establishment of the present climate stabilized the range of *Vipera kaznakowi* and allowed the joining of scattered populations from the refugia within the given region. The favorable conditions along the Black Sea coast made it possible for *V. kaznakowi* to disperse along warm river valleys up to midmountains and for *V. dinniki* to disperse along the northern slope of the Big Caucasus to the east up to the Belshaya Laba River head. Where *V. kaznakowi* and *V. dinniki* distributions meet, and those of *V. dinniki* and *V. ursini renardi*, zones of secondary hybridization emerged. In these zones the following is observed: intergradation of characters, a high degree of polymorphism, and the "plucking" of specimens from the "initial" type. In these populations the specimens are hard to define.

Phenotypical diversity is great with regard to the Mzymta River valley (Fig. 15). Non-identified individuals having characters of both *Vipera ursini renardi* and *V. kaznakowi* are known from a number of localities in the complex eastern range of these vipers. We think that the history of *V. darevskii* is also connected with the invasion of *V. kaznakowi* from the south during the Miocene and its further wide dispersal throughout the Caucasus. *Vipera kaznakowi* apparently used to inhabit the majority of the Maly (Small) Caucasus area, including the Adzharo-Imeretinsky, Meskhetsky, and Dzhavakhetzky ridges. The fact that this range did exist in the past is demonstrated by a relict population of *V. kaznakowi* that occurs in Baniskhevsky Canyon, Georgia and by the proposed distribution of the vipers along the Trialetsky Ridge (Bakradze 1969). The latter might be a link between the areas presently inhabited by the closely related

species, *V. kaznakowi* and *V. darevskii*.

In middle Pliocene, *Vipera kaznakowi* apparently invaded the Dzhavakhetzsky Ridge (the Mokrye [Wet] Mountains). At that time the hot, arid climate of the region was replaced by a more humid, cool climate. Later on, however, beginning with the middle Pleistocene, processes of aridization and glaciation caused the final degradation of forests (Agakhanyants 1981). By that time the diverged vipers were restricted to the highest places in the mountains where maximum humidity could be found. At the same time the newly formed steppe areas were actively invaded by *V. ursini eriwanensis* (Reuss 1935) from the Anatolyskoye Plateau. Later on the viper became widely distributed throughout the entire montane-steppe belt in the Small Caucasus and the Armyanskoye Plateau. At that site one more source of hybridization, including further form-building, evidently existed. The genesis of *V. darevskii* can be explained by the hybridization of *V. ursini eriwanensis* and *V. kaznakowi* that split from its major range in the vicinity of the Mokrye Mountains (Plate 3).

Apparently, introgression of genes from *Vipera ursini eriwanensis* which essentially surrounded a small Pleistocene population of *V. kaznakowi* was very substantial. Morphological propinquity of *V. darevskii* to *V. ursini eriwanensis* and *V. kaznakowi* support its possible hybrid genesis (Borkin and Darevsky 1980). It goes without saying that further ecological, ethological, cytological and biochemical research of these vipers is needed to prove it. Similarly, Agakhanyants (1981) explains the floristic richness of the region by a complex interaction of invaders from the south and north in the highlands of the Small Caucasus. Further aridization of the climate caused the mesophilic form of *V. darevskii* to ascend into the mountains. Ecological disconnection in the present high-altitude belts caused complete separation of *V. darevskii* and *V. ursini eriwanensis*.

The presence of "kaznakowi" -like

vipers in Lagodekhi and other regions of the Big Caucasus may be accounted for solely by changes in climate in refugia that preserved populations and further divergence in isolated montane canyons. A number of isolated populations might be modified due to hybridization with *Vipera ursini renardi* in a manner similar to the above listed scheme.

During the period of xerophytization in the Holocene, breaks within the range of *Vipera kaznakowi* occurred. At that time isolated populations existed over a long period. A number of populations in hydrophilous epochs to follow, would have been capable of connecting many times. This is supported by the restoration of the former forest belt after Holocene xerophytization (Galushko 1974; Kharadze 1974). Pleistocene glaciation obviously also influenced the emergence of isolated populations and changes in the distributional limits (Markov et al. 1965).

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Studies on Hynobiid Salamanders, With Description of a New Genus

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Abstract. -The types of *Hynobius chinensis* Günther, 1889, were reexamined and are redescribed; the known range in China is mapped. *Hynobius yiwuensis* Cai, 1985, is relegated to the synonymy of *chinensis*. *Hynobius retardatus* Dunn, 1923, of Japan, differs markedly from all other *Hynobius* and is here placed in a new genus (*Satobius*). The new genus is characterized and compared to the other eight genera of hynobiids.

Key words: Amphibia, Caudata, salamanders, Hynobiidae, *Hynobius*, *Satobius*, China, Japan.

Introduction

As part of our work on a handbook of Chinese amphibians and reptiles, we have had to re-study certain Chinese hynobiid salamanders described in the literature and consider their relationships to extralimital species, especially those native to Japan. This paper is a result of these current investigations and concerns the identity and distribution of *Hynobius chinensis* Günther, 1889, the taxonomic status of *H. yiwuensis* Cai, 1985, and the proper generic status of a Japanese species, *H. retardatus* Dunn, 1923.

Results and Discussion

1. Identity and Distribution of Hynobius chinensis Günther, 1889

In 1889, Albert Günther described *Hynobius chinensis* from two specimens collected in Hubei Province. Previously, *Hynobius* species had been known only from Japan and Korea, thus Günther's records from central China were quite isolated from the ranges of the then-known species. Since 1889, however, no other specimens of *Hynobius* have been reported from Hubei, despite much collecting there, leading Zhao and Hu (1983, English translation 1988) to suggest that either the locality data for Günther's specimens are wrong or that *chinensis* is not, in fact, a species of *Hynobius*.

We have examined Günther's two syntypes (British Museum [Nat. Hist.] numbers 1946.9.6.54 and .55, formerly catalogued as 1889.6.25-26). Both are females, as judged from the external appearance of their cloacae (the specimens are too hardened to examine internally).

Based on our examination of the types, *H. chinensis* is a true *Hynobius* as defined by Zhao and Hu (1984, English translation 1988). Since Günther's (1889) original description is brief, we provide the following redescription: Head large, its length from snout to gular fold longer than its width (15.2 x 10.6 mm; 12.8 x 9.5 mm); tip of snout rounded. Eyes are dorsolateral in position, slightly protruded; diameter of eye shorter than the distance from its anterior corner to the tip of snout; pupil rounded. Nostril between eye and tip of snout, and slightly closer to the latter; distance between nostrils slightly larger or equal to the distance between eyes. A "V"-shaped bulge on top of head. No labial fold. An indistinct gular fold. Angle of jaw just behind the posterior corner of eye. Both maxilla and mandible with tiny teeth. Tongue elliptical, large, almost covering the entire floor of mouth. Series of vomerine teeth "┐"-shaped, the outer branch comprising 6-9 and inner branch 11-15 teeth; the angle formed by outer and inner branches just beyond the anterior margin of choanae; inner branches much longer than the outer ones and extending backwards to the level of the middle of eye ball; the



FIG. 1. Map of central China illustrating all known localities for *Hynobius chinensis*. The inset shows the location of the more detailed map. Locality records in Zhejiang and Fujian provinces are noted by solid circles; the star-shaped symbol in Hubei Province is the type locality (Yichang). Other localities mentioned in the text are noted by hollow circles; some major cities are added for reference. The river mapped in Sichuan Province (upstream from Chongqing) that is continuous with the Chang Jiang (Yangtze River) is known variously as the Dajin, Dadu, and Min.

posterior ends of two inner branches close but do not meet at midline. Body short and stout; limbs well developed and tips of digits meet when limbs adpressed. Costal grooves 11, very prominent and meeting on ventral midline. Fingers four, 2-3-4-1 in order of length, the first finger almost equal in length to the fourth. Toes five, 3-4-2-5-1 in order of length. Digits flattened, free; without palmar and tarsal tubercles; no cornified covering on palms, tarsi, fingers, and toes. Tail length shorter than snout-vent length; tail compressed, but cylindrical at the base and pointed at the end, without crest on ventral edge and only slightly so on its dorsal side. Skin smooth. The dimensions cannot be re-measured due to the specimens' hardened condition; only head length and width can be given (above). Further details about the types are given in Zhao and Adler (1989). Cai et al. (1985) have described the embryonic development and larval features of *chinensis*.

Lectotype: We hereby designate BMNH 1946.9.6.54 as the lectotype of *H. chinensis*.

Type Locality: Günther (1889) stated that "two specimens were collected by Mr. Pratt at Ichang [=Yichang]." (Here and below, modern spellings of place names, where different, are given in brackets. All localities are mapped in Fig. 1.) A. E. Pratt explored China during 1887-1890 and summarized his experiences in a book (1892). As Günther noted in the appendix to Pratt's book, herpetological specimens were collected at various localities in Hubei and Sichuan provinces, and he repeated the "Ichang" locality for the two *Hynobius* specimens. Pope and Boring (1940), however, stated that "Mell ('29) claims that Pratt's records from 'Ichang' were collected in the mountains south of the Yangtze River near Changyang." Curiously, no such paper by Mell is listed in the bibliography of Pope and Boring's monograph, nor can we find such a statement in any of Mell's publications, so we are unable to verify the basis of Pope and Boring's information attributed to Mell.

In his book, Pratt (1892) mentioned finding salamanders only twice (pages 179 and 224) but both localities are in Sichuan: a lake above Ta-t sien-lu [=Kangding], at

14,070 feet elevation, and at Kia-ting-fu [=Leshan], both of which are localities far to the west of Yichang (see Fig. 1). Four other new species of reptiles and amphibians were described by Günther in his 1889 paper, all having "Ichang" as their type locality, and for these taxa the locality has never been questioned, to our knowledge. Thus, we are inclined to accept the type locality as stated by Günther, until new evidence comes to hand, although this locality is about 700-900 km west of the other known localities for this species (see Fig. 1 and below).

Distribution: Subsequent to Günther's report, several other specimens of *H. chinensis* have been reported. Here we summarize all known records (see Fig. 1):

Fujian: Kuantun [=Guadun, 27° 42' N 117° 50' E, a town at Mt. Wuyi], Ch'ungan Hsien [=Chong'an County, 27° 46' N 118° 01' E] (Pope, 1931).

Hubei: Ichang [=Yichang, 30° 42' N 111° 17' E] (Günther, 1889).

Zhejiang: Dachen, 29° 28' N 120° 06' E, 140 m, and Chalin, (both in Yiwu County, 29° 18' N 120° 04' E), Zhenhai, 29° 57' N 121° 42' E, and Xiaoshan, 30° 10' N 120° 15' E, (Cai, 1985; types of *H. yiwuensis*); Wenling, 28° 22' N 121° 22' E, 1500 ft., (Boring and Chang, 1933; Chang, 1933).

Boring and Chang's specimens from Zhejiang Province have been examined and their identifications verified. Cai's species, *H. yiwuensis*, is a synonym of *H. chinensis* (see section 2, below). Thus, *chinensis* is the only *Hynobius* found in mainland China, except for two species in the extreme northeast; three other species are endemic to Taiwan.

2. Taxonomic Status of *Hynobius yiwuensis* Cai, 1985

Cai (1985) described *Hynobius yiwuensis* as new, based upon a series of adults (16 males, 11 females), juveniles, larvae, and eggs from Zhejiang Province.

Unfortunately, he was unable to compare his specimens directly with the types of *H. chinensis*. Based on our comparison with those types, however, we believe that the two taxa are synonymous. We base our conclusion primarily on the six features used by Cai to diagnose his new form.

Vomerine Teeth. Cai described the length of the inner branch of vomerine teeth in *yiwuensis* as longer than that of *chinensis*, yet our examination reveals no significant difference. Moreover, the shape of the vomerine teeth series is very similar and the numbers of teeth in both the inner and outer branches are within the same ranges in the two forms.

Head and Body Proportions. Cai stated that in *yiwuensis* the head is much longer than broad, in contrast to Günther's measurements for one specimen in which the length was only slightly greater (11 x 10 mm). Our re-measurement of Günther's specimens, taking snout to gular fold as head length, shows that in both types of *chinensis* the head is much longer than broad (see measurements in section 1, above). Cai also claimed that *chinensis* and *yiwuensis* differ somewhat in body proportions, the latter being less stout. Our comparisons failed to notice significant differences, when relative sizes are taken into account.

Adpressed Limbs. In both types of *chinensis*, the tips of the digits touch when the limbs are adpressed, but Cai's diagnosis states that in *yiwuensis* the tips usually do not touch. However, in Cai's specimens there is variation in this character and in about one third of them the tips of the digits do meet.

Costal Grooves. In his diagnosis, Cai stated that *yiwuensis* has 10 costal grooves, in contrast to *chinensis* which has 11. We have confirmed the presence of 11 in the types of *chinensis*. However, in Cai's type series there are a few individuals having 11 costal grooves, as Cai himself even noted (1985, p. 110). In a series of ten specimens of *chinensis* from Wenling, about 160 km southeast of Cai's type

TABLE 1. Comparison of the genera of hynobiid salamanders. See text for further details.

	<i>Batrachuperus</i> *	<i>Hynobius</i>	<i>Liua</i>	<i>Onychodactylus</i>	<i>Pachyhynobius</i> *	<i>Pachypalaminus</i> *	<i>Ranodon</i> *	<i>Salamandrella</i>	<i>Satobius</i>
Distribution	Western China, Afghanistan, Iran	Japan, China, Korea, Mongolia, Eastern Siberia	Central China	Japan, Korea, Northeast China, Eastern Siberia	Eastern China	Japan	Northern China, Siberia	Japan, Siberia to East Europe, Mongolia, Northern China	Hokkaido (Japan)
Number of species	6	21	1	2	1	1	2	1	1
Costal grooves	12-14	11-14	10	13-14	13	13	12	14	11
Costal folds between toe tips of adpressed limbs	-2 to +1	-5 to +3	+1	-2 to 0	-4	-2 to 0	0	-4 to 0	+1 to +4
Tail length vs. head and body	t>h+b or t<h+b	t<h+b	t<h+b	t>h+b	t<h+b	t<h+b	t>h+b	t<h+b	t>h+b
Premaxillary fontaoelle	present	absent	present	present	absent	absent	present	absent	absent
Basibranchial radii	present	absent	present	present	present	absent	present	absent	absent
Vomerine teeth (o=position of internal naris)	 or 								
Vomer vs. parasphenoid	sutured	broadly overlaps	sutured	sutured	overlaps	overlaps	sutured	overlaps	sutured, may overlap tip
Lungs	reduced	present	reduced	absent	reduced	present	reduced	present	present
Chromosome number (2n)	62, 68	56, 58, 60	64	78	64	58	66	62	40
Larval duration	2-3 years	1 year	2-3 years	2-3 years	?	1 year	2-3 years	1 year	1 year or more
Habitat in non-breeding period	water	land	water	land	water	land	land	land	water or land

**Batrachuperus* includes *Paradactylodon*, *Pachyhynobius* includes *Xenobius*, and *Ranodon* includes *Pseudohynobius*. According to some authorities *Pachypalaminus* is a synonym of *Hynobius* (Nishio et al., 1987).

locality, the number of costal grooves varied from 10 to 12 (Chang, 1933).

Tail Proportions. Cai noted that the tail of *yiwuensis* is compressed, with fin folds especially distinct in the males, whereas Günther stated that *chinensis* was without a tail crest. Günther did not mention the sexes of his two specimens, which are both females (see section 1), and this was not known to Cai. Thus, we believe that the differences in the tail may be due to sexual dimorphism and, in addition, perhaps also to further elaboration of the crests during the breeding season.

Color Pattern. Günther's description was based on specimens that had been preserved for some time. Moreover, Cai noted that the color pattern changes during the breeding season, when it becomes lighter and mostly green in color. Nevertheless, our comparisons of the two forms do not reveal any striking

differences.

Further details of our comparison between the types of *chinensis* and Cai's specimens of *yiwuensis* are given in Zhao and Adler (1989). In summary, we believe that all of these specimens represent a single taxon which, because of the priority of Günther's name, must be designated *Hynobius chinensis*.

3. Generic Status of *Hynobius retardatus* Dunn, 1923

The identity of this Japanese species was first recognized by E. R. Dunn, who briefly characterized it (Dunn, 1923a) and soon described it in more detail (Dunn, 1923b). The animal itself had been known to Japanese biologists since at least 1907 under the names *Hynobius fuscus*, *H. lichenatus*, and *H. nigrescens*. These names, however, are now known to be properly applied to species found elsewhere

in Japan (*fuscus* is a synonym of *nigrescens*). Dunn (1923a) noted that *H. retardatus* was a "well-marked species" and, as knowledge of this animal increased in succeeding years, its distinctiveness from other *Hynobius* and hynobiids generally became more apparent.

In 1932, Makino reported that *H. retardatus* has a diploid somatic chromosome number of 40, but since the comparable numbers for most other hynobiids were not known at that time, the full significance of this very low number was not recognized. In fact, *retardatus* has by far the lowest number of chromosomes in the family Hynobiidae (Table 1). Only in 1943, with Sato's magnificent review of Japanese salamanders, in which he included a special comparative study of their chromosomes, could the matter be properly evaluated, and Sato himself (1943, p. 489) suggested that *retardatus* might be worthy of generic rank. Unfortunately, Sato's premature death in August 1945, during the atomic bombing of Hiroshima (for a biography of Sato, see Adler, 1989), prevented him from pursuing this matter. In subsequent years, additional data on anatomy, karyology, and biology have accumulated which further support the separation of *retardatus* into a new genus, which we name:

Satobius, new genus

Type Species: *Hynobius retardatus* Dunn, 1923a.

Content: A single species.

Diagnosis: A genus of hynobiid salamanders (family Hynobiidae) characterized by very long limbs and toes (tips of digits of adpressed limbs overlap +1 to +4 intercostal spaces in adults); a very long tail (in adults, 100 to 118% of head and body length combined); a long neck and small head; no premaxillary fontanelle or basibranchial radii; two short series of vomerine teeth arranged in transverse arcs between the internal nares; vomer sutured to anterior end of parasphenoid; lungs present; diploid (2n)

chromosome number of 40; larval duration of one year or more (neoteny sometimes occurs); and both terrestrial and aquatic habits in adults during non-breeding season.

These characteristics are discussed below and, for easy access, are tabulated for each of the nine genera of hynobiid salamanders (Table 1).

Costal Grooves. These vertical grooves on the side of the body correspond to the position of ribs and, thus, to trunk vertebrae; generally, the number of costal grooves that can be counted is one less than the number of trunk vertebrae.

The typical number of costal grooves in *S. retardatus* is 11. In the Japanese species of *Hynobius* the modal numbers of grooves range from 11 to 13 (Misawa, 1989) and some mainland species have as many as 14 (Dunn, 1923b). For species in other hynobiid genera, the modal numbers of costal grooves range from 10 to 14.

Adpressed Limbs. As a relative measure of limb length, the minimum distance between the tips of the digits is determined with the limbs adpressed along the sides of the body. Distances are then measured in intercostal spaces, the fleshy folds between adjacent costal grooves.

In metamorphosed adults of *S. retardatus* the intercostal distance between the digits of adpressed limbs is +1 to +4; that is, because the limbs and toes are very long, the digits actually overlap by one to four intercostal spaces. Proportionately, these are the longest limbs found in any member of the entire family. In species of *Hynobius*, this measurement ranges from 5 to +3; among hynobiids other than *Hynobius* and *Satobius*, the longest limbs are found in *Pachypalaminus* (-2 to 0), but the toes are shorter than those of *Satobius*.

Tail. The tail of *S. retardatus*, as measured from posterior angle of the vent, is longer than the combined measurements of head plus body length. In adults, tail length varies from 100 to 118% of head-body

length, whereas in all other hynobiids it is shorter except in *Ranodon* (about 100-120% of head-body length) and in *Onychodactylus* (about 100-115%). The tail lengths of *Hynobius* species are significantly shorter than the head-body length (60-80%); only in the adults of *H. nigrescens* does the tail occasionally equal head-body in length. Apparently in all hynobiids, tail length relative to head-body increases with overall size, so the numbers given here are all taken, for comparative purposes, from large adults.

Vomer and Vomerine Teeth. The paired vomer bones (or prevomers for those who deny homology to the vomer of mammals) of the palate bear teeth near their posterior edges. The relationship between the vomers and the parasphenoids lying posterior to them varies among hynobiid genera (Table 1). In *S. retardatus*, the posterior edge of the vomer is sutured to the parasphenoid and overlaps very little, if at all in some specimens, onto the palatal surface of the parasphenoid (Inukai, 1932; Sato, 1943). The two series of vomerine teeth extend broadly between the internal nares in two slight arcs which nearly meet at the midline; the overall length of this patch of teeth along the midline is about 30% of the width of the series.

The general pattern of these teeth is like those in the genera *Onychodactylus* and *Ranodon*, and quite unlike that in *Hynobius* where the vomers (and the vomerine teeth on their posterior surface) extend onto the parasphenoids to a degree varying from species to species. In some *Hynobius* this overlap is small (e.g., *H. leechii* and *lichenatus*) but in most it extends onto the palatal surface for from one-third to as much as one-half the length of the parasphenoids (e.g., *H. formosanus* and *sonani*) (Sato, 1943). Since the vomerine teeth are located on this edge of the vomer, in these *Hynobius* the vomerine series has a pattern wholly unlike that in *retardatus*, beginning at the nares and extending far posteriorly on the palate in the shape of a lyre (see Table 1). In *H. formosanus*, for example, the length of the vomerine teeth along the midline of the palate is fully twice

the total width of the two series (versus 30% in *S. retardatus*).

Chromosomes. Makino (1932) was the first to report that *S. retardatus* has a diploid chromosome number of 40, as confirmed by others (Azumi and Sasaki, 1971; Morescalchi, 1975). No other hynobiid is known to have fewer than 56. In Japanese species of *Hynobius*, the so-called pond-type species are $2n=56$ (*retardatus* is a pond breeder) and the mountain brook types are $2n=58$ (except *H. okiensis* where $2n=56$); *H. kimurai* is ordinarily $2n=56$, except in one population ($2n=60$) which may represent a separate species (Morescalchi, 1975; Morescalchi et al., 1979; Ikebe et al., 1989). The Korean *H. leechii* is $2n=56$ (Makino, 1934), but the chromosome number is not known for any of the Chinese species of *Hynobius*.

Recent studies by Japanese and Italian workers show that the karyology of *S. retardatus* is even more different from that of *Hynobius* species than the low number of chromosomes would suggest. The combined lengths of the chromosomes in the genomes of *Hynobius* species and in *retardatus* are nearly equal at the same degree of condensation, and the amount of nuclear DNA is also approximately equal (Morescalchi, 1975). Despite these similarities, there are important differences that set *retardatus* apart from species of *Hynobius*. Kuro-o et al. (1987, as modified in 1989) were able to compare chromosome pairs in four *Hynobius* (3 Japanese and 1 Korean species) and *retardatus*, using the R-banding technique (RBG method), allowing them to identify 18 of 28 pairs in *Hynobius* and 16 of 20 in *retardatus*. Based on this analysis, chromosome pairs 2 and 8 of *retardatus* are not at all represented in the genomes of these *Hynobius* species, whereas pairs 2, 12, 20, and 22, found in all four *Hynobius*, were lacking altogether in that of *retardatus*; other chromosome pairs were completely (11 pairs) or partially (3 pairs) homeologous. To summarize, among these four *Hynobius* species homeologies totalled about 90%, but this value fell to 65% when *retardatus* was included. DNA

analysis was also performed by these authors, using highly-repetitive DNAs as probes on Southern blot hybridization, which showed that *retardatus* was distinctively different from the five *Hynobius* species tested (4 Japanese and 1 Korean).

Breeding Biology. The reproductive biology of *S. retardatus* has been studied in detail (Sasaki, 1924; Makino, 1933; Sato, 1989 and references cited therein). The larval period is normally less than a year, but at high elevations can take more than one year. Neotenus individuals are well known (Sasaki, 1924). Adults breed in ponds and are terrestrial during non-reproductive periods. However, unlike species of *Hynobius* which remain on land while not breeding, *retardatus* often visits the water during non-breeding periods (Sasaki, 1924).

Distribution. *Satobius retardatus* is found only in Hokkaido, the northernmost of the main Japanese islands. No *Hynobius* are known from Hokkaido and, among hynobiids, only *Salamandrella keyserlingii* is found there.

Relationships. Historically, *S. retardatus* has been said to be most closely related to *H. nigrescens* of neighboring Honshu Island, Japan (Sato, 1943). Indeed, the two species are superficially similar in that, as adults, both are blackish in color with little pattern and both possess relatively long tails. However, on closer examination, these two species are fundamentally different. *H. nigrescens* is a large-headed and short-necked species, as are all *Hynobius*, when compared with *S. retardatus*. The skull of *nigrescens*, in particular the vomer-parasphenoid relationship and the pattern of vomerine teeth, are typical of *Hynobius* and unlike the situation in *Satobius*. Furthermore, the number of chromosomes and details of chromosome structure, based on both C-banding and R-banding methods, are distinctly different. In short, we believe that the similarities between *nigrescens* and *retardatus* are due to convergence and do not reflect close phylogenetic relationship.

Several of the diagnostic characteristics of *S. retardatus* are similar to those of members of the *Ranodon* group of hynobiids, which includes *Batrachuperus*, *Liua*, *Onychodactylus*, and *Ranodon* (Zhao and Hu, 1984). The suturing of the vomer and parasphenoid, the pattern of vomerine teeth, and the relative lengths of limbs and tail in *retardatus* are similar to the condition in one or more members of the *Ranodon* group, but in most other respects *Satobius* is clearly a member of the *Hynobius* group of genera: *Hynobius*, *Pachypalaminus* (synonymized with *Hynobius* by Nishio et al., 1987) and *Salamandrella* (for discussion of these two groups of genera, see Zhao and Hu, 1984). Within this group, the closest living relative of *retardatus* may be *H. leechii* of Korea and northeastern China, according to their chromosome structure; indeed, as Ikebe et al. (1989) point out, based on C-banding patterns, *retardatus* is more similar to the northernmost populations of *leechii* rather than those in the southern part of the Korean peninsula.

We suggest that the ancestral stock leading to *S. retardatus* was derived from a *Hynobius*-like ancestor and arrived in Japan from the mainland very early, before the formation of the Tsugaru Strait which later isolated Hokkaido from the southern Japanese islands. *Satobius* differentiated in Japan but was later excluded from the more southern Japanese islands by a later invasion of hynobiids from the mainland. Thus isolated by the Tsugaru barrier, *Satobius* further differentiated, yet retained some of its primitive characters, including a few today found only in the *Ranodon* group.

The long isolation from *Hynobius* has led also to the chromosomal differentiation described earlier (although retaining some similarities to *H. leechii* on the mainland). The great reduction in chromosome number in *retardatus* may be due in part to fusions, since the total composite lengths and DNA content are approximately the same as for the *Hynobius* genome (Kuro-o et al., 1989). However, in view of the many differences based on the C-banding and R-

banding studies mentioned above, the karyotype of *retardatus* cannot be explained by a simple mechanism of fusions alone.

Etymology. We take great pleasure in naming this new genus for Ikio Sato (1902-1945), who first recognized its distinctiveness from *Hynobius*. The name *Satobius* is derived in part from the stem of *Hynobius* (*hynis* [or *hynniss*], Greek for plowshare, the cutting part of a plow, and *bios*, life).

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Relationships Between Serum T_4 , T_3 , Cortisol and the Metabolism of Chemical Energy Sources in the Cobra During Pre-hibernation, Hibernation and Post-hibernation

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Abstract. -This study analyzed the variation of the serum thyroxine (T_4), triiodothyronine (T_3), and cortisol in the cobra (*Naja naja* Linnaeus) in pre-hibernation, hibernation, and post-hibernation. The variations were compared with the changes of indexes of cobra metabolism in those three periods, such as oxygen consumption, serum glucose, serum triglyceride, glycogen content of liver, and triglyceride content of fat bodies. From pre-hibernation to hibernation, the change of metabolic indexes of the cobra indicated that the metabolic rate tends to decline because of the very low levels of the three serum hormones in pre-hibernation and falling temperature. Low temperature during hibernation limited the activities of the three serum hormones which were rising at higher levels during hibernation. From hibernation to post-hibernation, the rising temperature allowed the three serum hormones to increase markedly, stimulating metabolism gradually. Therefore the metabolic rate of the cobra during post-hibernation tended to rise again. The metabolic indexes of the cobra in post-hibernation showed a significant increase in metabolic rate, which had close relation with the high levels of the three serum hormones. The indexes of metabolism of the cobra indicate that it is hepatic glycogen and not fat that hibernating cobras use as their main energy source.

Key Words: Reptilia, Serpentes, Elapidae, *Naja naja*, cobra, thyroxine, triiodothyronine, cortisol, metabolism, energy metabolites, chemical energy sources.

Introduction

Hibernation is an adaptive strategy of ectotherms for keeping out of the cold during winter. The metabolic rate of the hibernating reptiles is apparently different from that of active ones, as a result of physiological adaptation. The endocrine system and its close relation to metabolism may play an important role in physiological adaptation. Maher (1965) pointed out that the maximum metabolic response in lizards to thyroxine occurred at 3°C; Wilhoft (1966) found that injections of thyroxine in lizards increased their metabolism. Musucchia (1984) suggested that the injection of cortisol into hamsters during hibernation or hypothermia could achieve the same result as the injection of glucose, which might prolong the survival of hamsters under the same conditions. We consider that the metabolism of energy metabolites in hibernating snakes must have a close relation to the control of serum thyroxine (T_4), triiodothyronine (T_3), and cortisol. This study may provide a way to find the mechanism of snake hibernation

and guidance for maintaining snakes.

Methods

This study was carried out from September 1987 to May 1988. Cobras *Naja naja* (Linnaeus) used as experimental animals were captured at Changlou, Fujian Province, China. We studied serum T_4 , T_3 , and cortisol, and related indexes of metabolism in cobras during pre-hibernation, hibernation, and post-hibernation.

Cobra groups: 12 adult cobras (6 males, 6 females) were captured in May 1987, weighing 176-273 g. These cobras had been fed in our college snake garden for 4 months before the experiment. On September 9, 1987, 6 cobras were taken out of the snake garden and tested as a pre-hibernation group (Pre G). On October 2, 1987, the remaining 6 cobras were transferred from the snake garden into a dark cement pool with a perforated metal window above. The temperature in the pool was similar to the atmosphere. On

February 10, 1988, 3 cobras were taken out from the pool and tested as a hibernation group (H G), and on May 7, the last three cobras were tested as a post-hibernation group (Post G).

Determination of oxygen consumption: The oxygen consumption of each group was determined using the method of Dong et al. (1986) corrected by the authors.

Heart beats and respiratory state: Heart rate and respiratory state of each group were measured by routine methods.

Analysis of three hormones: Blood was drawn from the posterior vena cava. Serum T_4 , T_3 , and cortisol of each group were analyzed by radioimmunoassay by means of kits produced by the Institute of Shanghai Biologicals. Each sample was analyzed twice.

Analysis of serum energy metabolites: Serum glucose and serum triglycerides of each group of snakes were analyzed by clinical chemistry methods, and each sample was analyzed twice.

Analysis of hepatic glycogen: Fresh snake liver of each group was weighed and cut into pieces. After having been in boiling water for 5 minutes, the liver pieces were homogenized. The homogenate was in boiling water for another twenty minutes and filtered immediately. The filtered homogenate was mixed with 95% alcohol - A. R. (mean analysis reagent) to twice the volume and kept at room temperature for ten minutes before it was centrifuged for twenty minutes at 3000 rpm. The supernate was drawn out, the sediment (glycogen) soluble in hot water was estimated by the following calculation:

Hepatic glycogen (g/Kg(BW)) = total glycogen content in liver/body weight (BW)

Analysis of fat body triglycerides: Fresh snake fat bodies of each group was weighed and a small weighed part was homogenized in a fixed volume of n-heptane (C_7H_{16}). The fat tissue was extracted in this way three times.

Triglycerides of fat bodies extracted in n-heptane were analyzed by clinical chemical methods.

Triglycerides of fat body(g/Kg(BW)) = triglyceride content in fat body/body weight (BW)

Results

1. Variations of the three serum hormones during Pre G, HG and Post G

The levels of serum T_4 , T_3 , and cortisol of Pre G were the lowest in the three cobra groups. The level of serum cortisol of HG was markedly lower than that of post G. The levels of T_4 and T_3 of HG were not distinctly different from those of Post G (Table 1).

2. Variations of the oxygen consumption and energy metabolites during Pre G, HG and Post G

The oxygen consumption of the HG group was significantly the lowest of the three cobra groups. The oxygen consumption of Pre G was not significantly different from that of Post G.

The contents of serum glucose of both

TABLE 1. Experimental results of the three serum hormones and t tests.

Groups	N or N'	Serum T_3 (ng/ml)	Serum T_4 (ng/ml)	Serum cortisol (ng/ml)
Pre-hibernation (A, 22.9°C)	6	0.2303	0*	369.0
Hibernation (B, 13°C)	3	0.3607	0.700	1509
Post-hibernation (C, 24.9°C)	3	0.5467	1.233	6953
t_{AB} value	7	3.967*	4.399*	12.35*
t_{BC} value	4	1.767	1.153	2.808*
t_{AC} value	7	4.703*	4.792*	5.168*

* Too small to measure. **Significant at 0.05.

TABLE 2. Experimental results of oxygen consumption by energy substances, and t tests.

Groups	N or N'	Oxygen consumption (ml O ₂ /hr • kg(BW*))	Serum glucose (mg%)	Serum triglyceride (mg%)	Hepatic glycogen (g/kg(BW))	Fat body triglycerides (g/kg(BW))
Pre hibernation (A, 22.9°C)	6	127.6	193.9	102.9	47.99	10.29
Hibernation (B, 13°C)	3	54.9	50.40	18.73	0.3825	16.04
Post-hibernation (C, 24.9°C)	3	788.6	143.5	24.4	0.03084	17.61
t _{AB}	7	9.731**	7.742**	6.542**	2.680**	1.108
t _{BC}	4	2.791**	5.473**	0.679	2.985**	0.1615
t _{AC}	7	2.316	2.220	2.165	2.699**	1.736

* BW = Body Weight. **P < 0.05

Pre G and Post G were apparently higher than that of HG. But the content of serum glucose of Pre G was not significantly different from that of Post G.

The hepatic glycogen content of the cobras appeared to decline during hibernation. The hepatic glycogen content of HG was markedly less than that of Pre G, and the hepatic glycogen of Post G was less than that of HG.

Similar to the variation of serum glucose, the content of serum triglycerides of Pre G was higher than that of HG, but there were not significant differences between the serum triglycerides of post G and that of HG, and between that of Pre G and that of Post G. The triglyceride contents of fat bodies in the three cobra groups did not have any statistical differences from one another (Table 2).

Discussion

1. Variations of the oxygen consumption and energy metabolites in the cobras during the three periods

The contents of serum glucose and triglycerides of Pre G were relatively high due to the cobras active intake before entering hibernation, which was

advantageous for the storage of energy metabolites for overwintering. The oxygen consumption was large during this period, but the contents of glucose and triglycerides of HG were apparently at low level. Oxygen consumption decreased markedly in this period. The hepatic glycogen content during hibernation became 99% less than during pre-hibernation. The triglyceride content of fat bodies of the HG group seemed to rise a little, perhaps due to some triglyceride synthesis at the beginning of hibernation.

These results indicate that the metabolic rate of cobras during hibernation remains at a low level and oxygen consumption, serum glucose, and serum triglyceride content fell markedly, and that hepatic glycogen is used as the main energy source instead of fat body triglycerides. In post-hibernation, the serum glucose content rose significantly and the content of hepatic glycogen decreased by 92 percent less than that of HG, showing that cobras had used hepatic glycogen to the greatest degree for evoking their activities. This variation provided a good situation for cobras to come out from hibernation, and at the same time, oxygen consumption increased greatly. The rising serum triglycerides of post G also meant that the cobras' fatty metabolism began to become active.

Compared with that of pre G, the oxygen consumption of post G was relatively large, but the serum glucose and serum triglyceride content of post G were relatively low. The reasons may be: 1) that the pre G cobras were not fasting so that their contents of serum glucose and triglycerides were relatively high, 2) that the post G cobras had so little hepatic glycogen as to be unable to raise their serum glucose and triglyceride contents as high as those of the Pre G group, and 3) that the rising temperature and the high serum hormone level after hibernation accelerated the organs and tissues to take in glucose and triglycerides from the blood. Among the three reasons the latter was the most important because of the apparent rise in oxygen consumption. This amount indicated that the metabolism in the organs and tissues had been enhanced markedly.

2. Variation of the three serum hormones

Serum T_3 of HG was 56.6% higher than that of Pre G, and serum T_3 of Post G 51.7% higher than that of HG. Similar to serum T_3 , serum T_4 of Pre G was too low to be tested, but T_3 of HG rose significantly, and T_3 of Post G continued to rise 43.2% more than that of HG. As a result, serum T_3 and T_4 were increasing steadily during hibernation. This pattern of serum T_4 was similar to the results reported by Nauleau, et al. (1987).

A comparison between the variations of serum T_3 and serum T_4 can provide some important information about the secretive state of the thyroid gland. Before hibernation, serum T_4 was very low, and serum T_3 was higher, being in a dominant position, but in hibernation, serum T_4 was twice as great as serum T_3 , though both of them had increased. These variations were caused by the increased activity of the thyroid gland during hibernation. Turner and Bagnara (1976) suggested that the activity of the thyroid gland of ectotherms was low both in summer and during pre-hibernation. It was enhanced during hibernation, reaching a peak during post-hibernation. The thyroid gland mainly secretes T_4 , which is the precursor of T_3 .

The secreted T_4 is converted into T_3 in the blood or in the tissues and organs. The function of stimulating metabolism by T_3 is at least three times stronger than that by T_4 . The activity of the cobra thyroid gland was at a low level in pre-hibernation. The synthesized and secreted T_4 was very low and a portion of T_4 was converted into T_3 thus the concentration of serum T_4 was at a low level and the level of T_3 was relatively high. After the cobra entered hibernation, the secretive function of the thyroid gland began to become active and produce more and more T_4 , therefore serum T_4 dominated at a higher level though both T_4 and T_3 increased in the blood. The variation of serum T_4 and T_3 in post G was the same as in HG. The very high levels of serum T_4 and T_3 in post G were of great advantage to the cobra enhancing its metabolic rate for arising from hibernation. Besides these, the results in Table 1 and Table 2 also indicate that the levels of serum T_4 , and T_3 , of HG were higher than that of Pre G, but the amount of oxygen consumption of HG was less than that of Pre G. This seemed to be self-contradictory because both T_4 , and T_3 , were able to stimulate metabolism. These phenomena resulted in the falling temperature, inhibiting the function of hormones. Wilhoft (1966) pointed out that the function of T_4 stimulating metabolism appeared to be inactive in many reptiles at low body temperature, and to be active only at higher temperature. Stimulation of metabolism was carried out in such a way that T_4 and T_3 were capable of inducing the synthesis of aerobic metabolic enzymes. The low levels of serum T_4 and T_3 in pre-hibernation indicated that the metabolic rate of cobras in this period tends to fall.

The metabolic enzymes which had been synthesized were still in an active state because of the higher temperature, thus the pre G cobras had a high oxygen consumption. The metabolic rate of HG, though serum T_4 and T_3 levels had risen, was at a low level due to the low temperature during hibernation which inhibited the function of T_3 (T_4) and the activity of metabolic enzymes synthesized before. The cobras of HG had a small oxygen consumption. The very high levels

of serum T_4 and T_3 gradually performed the function of stimulating metabolism in the phase at the end of hibernation as the temperature was rising.

Serum cortisol was increasing continuously during hibernation. Serum cortisol of HG was 2.8 times higher than that of pre G, and that of post G which continued to rise by 3.6 times more than that of HG. Musacchia (1984) reported that the survival of animals during hibernation or hypothermia had a close relation to the level of serum cortisol in their bodies. An injection of cortisol into hamsters during hibernation or hypothermia could yield the same result as an injection of glucose, and might increase the survival of hamsters under the same conditions. He also reported that glucocorticosteroids played an important role in animals arising from hibernation or hypothermia. Some clues perhaps could be found for reptiles from the experimental results on hamsters, although they were very different in other respects.

The results in Table 2 indicated that the hepatic glycogen content of HG was very low. It was difficult for cobras to continue hibernating while only using so little an amount of hepatic glycogen as a energy source. They must receive energy metabolites in other ways. Gluconeogenesis may be an important process in which cortisol has a close relation. The suprarenal cortex of cobras during hibernation became active gradually and the level of serum cortisol became higher and higher, which was related to accelerating gluconeogenesis and to the cobra's arising from hibernation. The variation of cortisol showed that fat metabolism became active after cobras were aroused out of hibernation.

3. Relationship between the three serum hormones and energy metabolites

In pre-hibernation, the function of T_4 and T_3 in inducing synthesis of aerobic metabolic enzymes was weak because of the low levels of serum T_4 and T_3 . The metabolism of cobras in this period was

under the control of the enzymes which had been synthesized before. The metabolic rate of cobras tended to decrease from pre-hibernation to hibernation as the temperature was falling and as the amount of enzyme reduced (synthesizing less and degrading). During hibernation, when the temperature was low, cobras had a low metabolism under the control of the low-temperature isozymes, though the levels of serum hormones were at relatively higher. The low serum glucose and triglyceride contents implied that the decreased metabolism of cobras in hibernation, and the reduction of glycogen in the liver indicated the metabolic rate of cobras at a certain level. In post-hibernation, high temperature provided a favorable factor for hormones to perform their functions, and T_3 (T_4) induced synthesis of enzymes and cortisol accelerated the gluconeogenesis and fat catabolism. Serum glucose was increasing markedly though the hepatic glycogen was low, and quite a lot of glucose was produced from gluconeogenesis. Serum T_4 and T_3 play an important role in accelerating somatic cells to take in energy metabolites and in raising metabolism.

In short, during hibernation the cobra nearly used up all the hepatic glycogen but consumed little fat body triglyceride. Body weight tended to be lost significantly during the period after the snake was aroused out of hibernation. Perhaps fat bodies were used up because there was little hepatic glycogen. The high level of cortisol indicated the tendency for fat catabolism.

4. One putative pattern

From the above results, we consider that perhaps the cobra has formed a seasonal regulation of endocrine and that hibernation is controlled by this mechanism. When the season for hibernation comes, the contents of serum T_4 , T_3 , and cortisol decrease so that the metabolic system of all organs and tissues in cobras is controlled effectively. The metabolic rate of cobras tends to go down. With temperature falling and the three serum hormones reducing, the remaining metabolic enzymes in cobras

become inactive gradually (content less and activity low) and cobras go into hibernation keeping their metabolic rate at a fairly low level under the control of the low temperature isozymes, and after physical regulation. This suggests that the external factor for cobra hibernation is the fall of temperature, while the internal factor is the drop of the three serum hormone levels. In hibernation, the contents of serum T_4 , T_3 , and cortisol increases gradually, but the levels of the three serum hormones are not high enough to accelerate metabolism of the organs and tissues, and the low temperature inhibits the activities of the three serum hormones. When the levels of serum T_4 , T_3 , and cortisol are high enough, the metabolism of the organs and tissues in cobras tends to go up. With the temperature rising, the three serum hormones induce the synthesis of aerobic metabolic enzymes in the organs and tissues and accelerate the metabolism of energy metabolites. The metabolic rate rises and the cobra recovers from hibernation. This suggests that the external factor for the cobra to come out of hibernation is the rise of temperature, while the internal factor is the rise of the three serum hormone levels.

5. Conclusion

Serum T_4 , T_3 , and cortisol at low levels were involved in the regulation of depressing the metabolism of cobras before hibernation. The low temperature during hibernation inhibited activity of the three serum hormones, and the metabolism was at a low level. With the rising temperature, the levels of serum T_4 , T_3 , and cortisol at very high levels accelerated the metabolic rate of cobras which resulted in arousal from hibernation. Cobras in hibernation used hepatic glycogen as their main energy source instead of fat body triglycerides.

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Intergradation Between *Melanochelys trijuga trijuga* and *M. t. coronata*
(Testudines: Emydidae: Batagurinae)

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Key words: Reptilia, Testudines, Emydidae, *Melanochelys*, India, distribution, intergrade.

The Indian Black Turtle or *pe amai*, *Melanochelys trijuga*, is one of the most abundant chelonians in the Indian subcontinent, with a distribution extending from Sri Lanka (Deraniyagala 1939), through India and Burma, to western Thailand (Wirot 1979), although apparently excluding Bangladesh (Das, 1989). Nevertheless, details of the distribution of the seven described subspecies remain obscure. The range maps provided by Smith (1931), Das (1985), and Tikader and Sharma (1985) indicate rather clearly allopatric distributions for the Indian subspecies, but the overall range of the species is based on extremely few and widely-separated locality points (except for Sri Lanka and Kerala), as is evident in the map provided by Iverson (1986). Deraniyagala (1939) recognized two subspecies in Sri Lanka, but the geographic separation, if any, between these two forms was not made clear.

Of the various subspecies, the most distinctive is probably *Melanochelys trijuga coronata*, whose distribution is restricted to the state of Kerala in southwestern India (the distribution map provided by Tikader and Sharma (1985) involves a transposition of the range of *coronata* and *trijuga*). *M. t. coronata* has a striking head pattern, with a broad, black diamond-shaped marking on the crown of the head, contrasting with the white to yellow temporal region. The head pattern of the other subspecies consists at most of small, yellow to pink spots and reticulations that may disappear with age. The shell as a whole is usually unrelieved black, in contrast to other subspecies in which at least a lighter plastral rim is evident (although Deraniyagala (1939)

reported completely black specimens of *M. t. trijuga* from Kalpitiya, Sri Lanka and we have seen increased pigmentation with age in the north Indian subspecies, *indopeninsularis*, in which adult animals may lose the lighter plastral rim). The distribution of *M. t. coronata* is generally indicated as widely separated from that of *M. t. trijuga* by the Western Ghats, but the southward penetration of the *forma typica* into the hiatus between these two subspecies is not represented on existing range maps, and the subspecific relationship between these two forms has been assumed rather than demonstrated. We here report upon four specimens that bridge the geographic map between *M. t. trijuga* and *M. t. coronata*, and three that show characters intergradient between them.

An adult male (CL 23.9 cm; CW 16.4 cm) was collected by the two authors from a dry stream bed in Chichli, Indira Gandhi (formerly Annamalai) Wildlife Sanctuary, Coimbatore District, Tamil Nadu, on March 27, 1989 (Fig. 1). The right anterior margin of the shell showed signs of an old injury, with several peripheral bones lost. The head pattern of the specimen included the diamond-shaped marking typical of *Melanochelys trijuga coronata*. The yellow head reticulations and the yellow plastral margin is suggestive of *M. t. trijuga*, and the size of the specimen is greater than that of any recorded specimen of *M. t. coronata* (maximum 17.5 cm (Smith 1931) or 18 cm (Tikader and Sharma 1985) of 20.8 cm (Das 1985)). The specimen was retained alive and housed at the Madras Crocodile Bank.

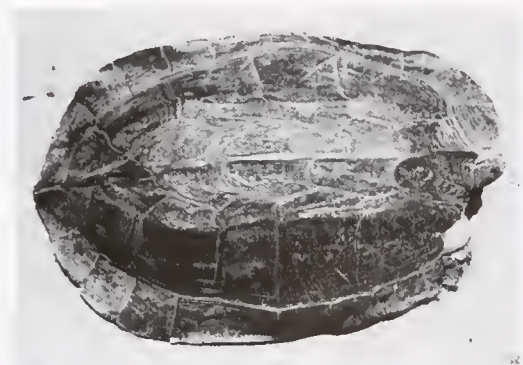


FIG. 1. Intergrade between *Melanochelys trijuga coronata* and *M. t. trijuga*.

A second specimen—a fragmentary shell only—was also found in the Indira Gandhi Wildlife Sanctuary, in a tribal settlement. The nuchal area and anterior peripherals are missing. Shell width is 13.7 cm, again indicating a specimen larger than is typical of *Melanochelys trijuga coronata*. Ankylosis of the shell, as illustrated for Sri Lanka specimens by Deraniyagala (1939), is essentially complete, except for faint indications of the peripheral sutures. The specimen is registered as PCHP 2803 in the private collection of the second author.

In addition to these, two intergradient specimens were found in the collection of the Southern Regional Station of the Zoological Survey of India (Madras), both collected by M. Vasant and party. An 8.1 cm juvenile (Lot no. 10) was collected at Kombiar Charagam, Kalakkadu Wildlife Sanctuary, Turunelveli District, Tamil Nadu (altitude 210 m), on October 13, 1987. A 20.6 cm adult male (Lot no. 6) was collected at Nambiar, Nambi Kovil Road, also within Kalakkadu Wildlife Sanctuary (altitude 140 m), on January 11, 1987.

Melanochelys trijuga is basically a pond turtle, and the Western Ghats appear to separate the essentially lowland ranges of *M. t. coronata* and *M. t. trijuga*. Nevertheless, the new localities all fall within upland areas actually in the Western Ghats. It appears that the hills may form a sufficient barrier to allow the evolution of

different subspecies east and west of the Ghats, but the ability of *M. trijuga* to exist far from water suggests that individuals wandering into these hills may provide the stock for an intergradient population. It would be worthwhile to search for a lowland intergradient population in the coastal area at the northern extreme of the distribution of *M. t. coronata*.

Other cases exist of congeneric batagurine species of a similar ecological role differing primarily in head pattern, as is the case with some of the species of *Rhinoclemmys* in the Neotropics. One is tempted to interpret the different markings as a means of avoiding cross-matings in situations of sympatry. But, the overall allopatry of the species of *Rhinoclemmys* in northern South America, for example, suggests that this interpretation may be an incomplete one, as does the discovery of intergradation between adjacent populations of *Melanochelys* that differ primarily in cephalic pigmentation.

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Thermal Sensitivity of Sprinting and Clinging Performance in the Tokay Gecko (*Gekko gekko*)

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Abstract. -The thermal sensitivity of sprinting and clinging ability was measured in tokay geckos (*Gekko gekko*). Sprinting performance was maximal at high (35-41°C) temperatures, as is the case for other nocturnal lizards, but the optimal temperature for clinging was considerably lower (approximately 17°C). These different optima could be adaptive if maximal sprinting and clinging capabilities are needed at different temperatures. Alternatively, they could result from constraints on adaptive evolution.

Key Words: Reptilia, Sauria, Gekkonidae, *Gekko gekko*, thermal sensitivity, optimal performance.

Introduction

Most physiological processes are temperature-dependent. Ectothermic animals, which do not maintain a constant body temperature, are thus subject to fluctuation in the rate at which they can perform many vital tasks. By regulating body temperature behaviorally, however, many reptiles can maximize performance capability (Huey 1982a). In some cases, maximal performance temperature might differ for different tasks. For example, a wealth of behavioral data indicates that many lizards and snakes increase their body temperature after feeding, which suggests that digestion has a higher optimal temperature than other activities (reviewed in Huey 1982a).

Early work centered on the thermal dependence of sub-organismal traits (e.g., enzyme activity, muscle contractile speed [Huey and Stevenson 1979]). In many cases, however, the effect of temperature on the functional capacities (e.g., sprint speed, critical thermal maximum temperature) cannot be predicted by study at sub-organismal levels (e.g., Licht 1967; Marsh and Bennett 1985, 1986). Consequently, recent studies have focused on whole-organism performance. The thermal dependence of sprinting ability has been studied in great detail. Maximum sprinting speed and/or endurance in many species occurs at the temperature they most

frequently experience in nature (Bennett 1980); however, nocturnal lizards appear exceptional (Huey and Bennett 1987; Huey et al. 1989). The thermal sensitivity of few other whole-organism locomotor performance measures has been determined for lizards. Here I report the thermal sensitivity of tokay geckos (*Gekko gekko*) [Fig. 1] for two ecologically relevant tasks, maximum sprinting and clinging capability. I ask whether maximum performance capability occurs at the relatively low temperatures most commonly experienced by geckos (Huey et al. 1989) and whether the optimal temperature is the same for the two performance measures.

Methods

Tokays are relatively large geckos found on trees and walls throughout southeastern Asia (Smith 1935). Lizards were captured on Phuket Island, Phuket Province, Thailand, and transported to the University of California, Berkeley in late September 1987. They were maintained in 30 x 17 x 9 cm plastic shoeboxes at ambient temperatures and provided with water and crickets *ad libitum*. An ontogenetic series was used in this study (11 individuals; snout-vent length: 85-180 mm; mass: 10-140 g).

All trials were conducted in a walk-in environmental chamber in the Museum of Vertebrate Zoology, University of



FIG. 1. *Gekko gecko* from Phuket Province, Thailand.

California, Berkeley. within a month of capture. Lizards were placed in the chamber at least one hour prior to performance measurement. Humidity, which could not be regulated, was determined on several occasions using a Bacharach sling psychrometer.

Clinging capability was measured by placing lizards on a plexiglass plate and, at a gradual and steady rate, lifting the end of the plate so that the lizard was clinging with its head directed down. The angle at which the lizard fell from the plate was recorded (protocol modified from Emerson and Diehl 1980; Alberch 1981). Lizards that jumped from the plate were not included in the analysis. As lizards began to slide, they usually attempted to maintain their grip by moving and re-applying their toe pads regardless of temperature. There was no evidence that temperature affected the lizards' efforts to prevent sliding and falling

from the experimental plate.

One trial per lizard was conducted per temperature. Performance at nine temperatures (12, 16, 17, 22, 24, 31 [three times], 34, 35, 41; the order of temperatures is presented in figure 2) was measured over a six-day period. On some days, two trials were conducted.

Sprint capability was measured by placing lizards at the end of a 2.25 m trackway covered with a rough rubber surface and inducing them to run by repeated taps to the tail (protocol following Huey 1982b; Huey et al. 1989; Garland 1985). As the lizard ran, it interrupted light beams stationed every 0.25 m. The time elapsed during each interval was computed by a Compaq personal computer; the fastest single interval during four trials, conducted at hourly intervals, was considered the maximum speed for that lizard at that

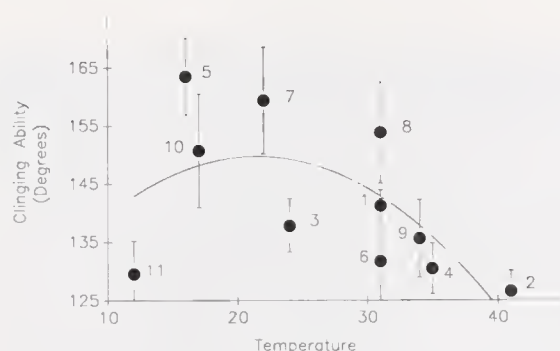


FIG. 2. Clinging ability (mean $\pm$ 1 s.e.) at different temperatures. Clinging ability is measured as the angle of the plate at which a lizard lost its grip and fell. The points are numbered by the order in which the trials were conducted.

temperature. Lizards that did not sprint at maximal capability on any of the trials at a given temperature, as judged by their gait, were not included in the calculations for that temperature. Lizards were tested at five temperatures (30, 36, 19, 26, 41°C, in that order), one temperature per day, over an eight-day period. Trials were never held on three consecutive days. A second trial at 30°C was held at the conclusion of the study to determine whether a performance decline had occurred. Animals whose performance decreased $> 30\%$ were excluded from the analysis.

Results

Clinging performance is temperature-dependent, with a peak at 17°C (Fig. 2). A non-linear equation ($\ln [\text{clinging ability}] = 0.99 + 2.69 * \ln [\text{temp}] - 0.45 * \{\ln [\text{temp}]\}^2$; $F_{2,8} = 5.08$, $P < 0.05$) better fits the data than a linear regression ($F_{1,9} = 2.77$, $P > 0.10$).

Although between-day variation exists in clinging ability at a given temperature, no general pattern of increased or decreased performance over the duration of the study exists. For example, three trials were conducted at 31°C. The second trial had the lowest mean, whereas the last trial had the highest mean. Three other sets of trials were conducted at approximately the same temperature (16-17°C, 22-24°C, 34-35°C). In two cases, performance ability decreased

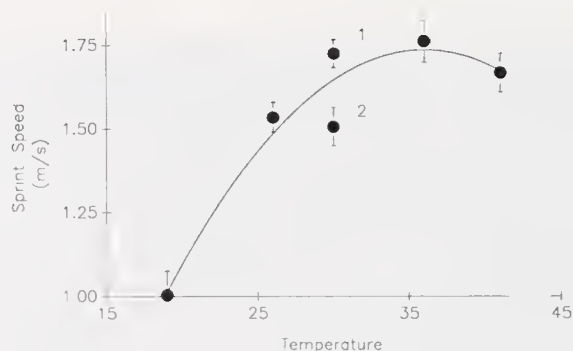


FIG. 3. Sprint speed (mean $\pm$ 1 s.e.) at different temperatures. The numbers indicate which represents the first and the second 30° trials.

in the second trial, but in the third case it increased.

Sprinting capability is also temperature-dependent (Fig. 3). Maximal performance ability occurs at 36-41°C, but interpretation of the results is difficult because performance ability declined over the course of the experiment, as evidenced by the difference in sprinting ability in the two sets of trials at 30°C. Despite this decline, several results are clear from inspection of Fig. 3: 1. performance at 36°C (tested 8 July) is slightly higher than at 30 (7 July); performance at 40°C (tested 13 July, after all trials except the second set at 30) is nearly as high or higher than all other temperatures; 3. performance at 30°C (16 July) is greater than performance at 26°C (11 July), which, in turn, is greater than performance at 19°C (10 July). Consequently, even if performance steadily decreased over time, it is reasonable to conclude that maximal sprint performance occurs around 36-41°C.

Discussion

Sprinting and clinging are ecologically relevant performance measures for geckos, but their optimal performance temperatures differ greatly for tokays. Sprint performance is greatest at relatively high temperatures, as is the case for a number of other nocturnal gecko species (Huey et al. 1989) and the nocturnal skink

Eremiascincus fasciolatus (Huey and Bennett 1987). Clinging capability, the thermal dependence of which has never previously been investigated, is maximal at considerably lower (approx. 17°C) temperatures.

It is difficult to envision how such different optima could evolve adaptively. Most lizards sprint maximally at temperatures close to those they normally experience (Huey 1982a; Huey et al. 1989). The low optimal temperature for clinging matches the field temperatures of many active nocturnal geckos (Huey et al. 1989). However, many nocturnal geckos bask and/or are active to some extent during the day (Bustard 1967, 1968; Werner and Whitaker 1978; Nagy and Knight 1989). Consequently, the high optimal temperature for sprinting seen in many nocturnal lizards might represent adaptation for diurnal capability (Huey and Bennett 1987; Huey et al. 1989). Nonetheless, it seems implausible that one aspect of locomotion, sprint performance, should be selected at high temperatures, whereas another important component of effective movement, clinging, should be favored at considerably lower temperatures.

As an alternative explanation, the differences in thermal optima might result from differences in evolutionary lability of the two performance capabilities and thus represent constraints on adaptive evolution in either sprinting or clinging ability. To understand why these performance abilities are affected differently by temperature, a better understanding is needed of their underlying physical and physiological bases (e.g., Garland 1984, 1985; Marsh and Bennett 1985, 1986). In many species of lizards, sprint performance is maximal at temperatures close to the critical thermal maximum (Huey and Bennett 1987; Huey et al. 1989). The cause for this linkage is unclear. However, if geckos must be able to survive diurnal temperatures (either because they intentionally maintain high temperatures to maximize other processes, or because environmental conditions preclude the maintenance of lower temperatures), then they would have to

evolve high critical thermal maxima. The high sprint performance maximum might be a correlated effect of this physiological adaptation to high temperatures and not be adaptive per se (Huey et al. 1989).

Clinging capability depends upon both physical and physiological processes. Geckos cling to smooth surfaces by dry adhesion. The subdigital lamellar pads of geckos are covered with millions of microscopic setal hairs. When the pads are adpressed to a surface, these hairs form intermolecular bonds with molecules on the surface of the substrate (Hiller 1975). If the surface energy (a measure of the number of free electrons on the surface of the substrate) is relatively high, then enough bonds can form to support the lizard. Because these bonds result from the activity of electrons, the forces theoretically should be temperature-independent over the range of temperatures in this study.

However, geckos have an elaborate muscular and vascular system for the adpression and removal of their toe pads (Russell 1975); the thermal dependence of these muscles has not been investigated. The poor clinging performance of geckos at 10-12°C is clearly the result of physiological incapacitation. At that temperature, geckos were generally inactive, moved slowly and infrequently, and even rarely bit or barked when handled. In contrast to trials at higher temperatures, the lizards did not attempt to adjust their pads or posture when the plate was tilted and quickly lost their hold. More research is required to determine whether the performance decline at temperatures above 17-18°C results from decreased capability of the muscles and enzymes involved in clinging.

One possible confounding effect in the clinging experiments is the variation in absolute humidity. Moisture might decrease the formation of high-energy intermolecular bonds. Absolute humidity in the environmental chamber was measured at several temperatures and increased from 8.5 Barrs at 11.9°C to 25.1 Barrs at 34.3°C (relative humidity,

however, was greatest at intermediate temperatures). Consequently, the greater absolute humidity at higher temperatures in the environmental chamber might have caused a decrease in clinging ability. Further research is needed to investigate to what extent humidity affects clinging.

Although different processes may often be maximized at different temperatures, rarely is the difference as great as is observed between sprinting and clinging in tokay geckos (Huey 1982a). One would not expect these geckos to need maximum ability at these aspects of locomotion at such different temperatures, but neither would one expect the physiological sensitivity of different systems to be so different. Interestingly, the optimal temperature for hearing sensitivity in the tokay gecko is intermediate between the sprinting and clinging optima (Werner 1976). Further research is required to understand the processes shaping and constraining performance evolution.

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Mating Call Structures of the Chinese Frog, *Rana nigromaculata* (Amphibia, Anura, Ranidae)

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Abstract. -Mating calls of the Chinese Pond Frog, *Rana nigromaculata* at three localities were recorded and compared. The calls of *R. nigromaculata* are short in duration and consist of a few notes. Each note has several distinct pulses. The call structures of northern and central China are different from those of Sichuan, hence we tentatively regard them as different subspecies.

Key words: Amphibia, Anura, Ranidae, *Rana nigromaculata*, mating calls.

Introduction

Rana nigromaculata occurs widely in the lower Amur and Ussuri river valleys (USSR), Korea, Japan, and throughout northeastern and midwestern China. In China it occurs in all but Xinjiang, Tibet and Guangxi autonomous regions, and Yunnan, Taiwan, and Hainan provinces. As far as we know, no paper has been published in China analyzing the mating calls of Chinese anurans.

The mating call of frogs is a useful clue in revealing systematic and evolutionary relationships. Vocalizations are species-specific in anurans, and serve as isolating mechanisms. Therefore, some taxonomic revisions have been based primarily on call differences [see Kuramoto (1977) for review].

Methods

Calls of *Rana nigromaculata* were recorded in 1988 at three localities. Several calls of a single male were recorded on 19 March, in the suburbs of Hongya County, about 100 km southwest of Chengdu, Sichuan Province. The frog was calling from a stone near water. The water temperature was 19°C.

A number of calls from three males were recorded at East Lake Park, Wuchang, Wuhan, Hubei Province on 17 June. The frogs called while standing in shallow water shaded by grass. The water

temperature was 22°C.

The calls of 10 males were recorded at Wofoshi, Xiangshan Park, Beijing, on 28 May. Male frogs were found calling in surroundings similar to those of frogs in Hubei Province. The water temperature was 24°C.

Temperature records were always taken in the vicinity of calling males. Calls were recorded with a Sony TCS-370 cassette recorder and a Feidec TSM-91 microphone. Sonograms were prepared with Kay 7800 and Kay 7900 sonographs. For the analysis of mating calls, standard (2.56 sec) sonograms with a 150 Hz bandwidth filter were used.

When a call was composed of several groups of pulses, each group was termed a note. The main acoustic parameters measured were: duration of call, number of notes and pulses, pulse repetition rate (number of pulses per second), fundamental frequency, and dominant frequency.

Results and Discussion

The vocalizations of *Rana nigromaculata* consist of 4-10 notes, and each note has 3-7 distinct pulses. The higher frequency parts (above 2 kHz) are usually absent in the first few notes (1-3). Time intervals between pulses tend to become longer at the end of the call. In all localities, the frog's frequency band ranges from 0 to 8 kHz.

TABLE 1. Analysis of the calls of *Rana nigromaculata*. The dominant frequency and pulse repetition rate of *R. nigromaculata* from Hongya, Sichuan are about half of those recorded at the other localities. Note the divergence of the Sichuan call structure from northern (Beijing) and central (Wuhan) China.

Number of Notes	Call Duration	Pulse Repetition Rate	Number of Calls	Fundamental Frequency	Dominant Frequency
Beijing					
10	668.6	89.7	1	0.53±0.02	2.39±0.20
9	529.9±77.1	84.7±10.8	3		
8	450.5±26.4	80.6±27.4	12		
7	396.4±21.0	109.8±44.0	7		
6	344.7±33.1	104.7±22.1	6		
5	324.2±17.9	84.5±26.2	3		
4	255.0±35.8	43.2±11.2	5		
1	50.8±12.1	154.8±45.9	5		
Wuhan					
8	467.3	69.3	1	0.51±0.09	2.32±0.17
7	452.6	86.2	1		
6	426.6±53.6	77.7±8.7	3		
5	319.7	90.7	1		
1	50.8±17.5	120.8±34.1	10		
Hongya					
5	637.6±66.9	45.4±7.7	7	0.47±0.06	1.42±0.10
4	576.5±57.0	49.8±5.5	7		
1	79.9±13.1	125.4±2.1	2		

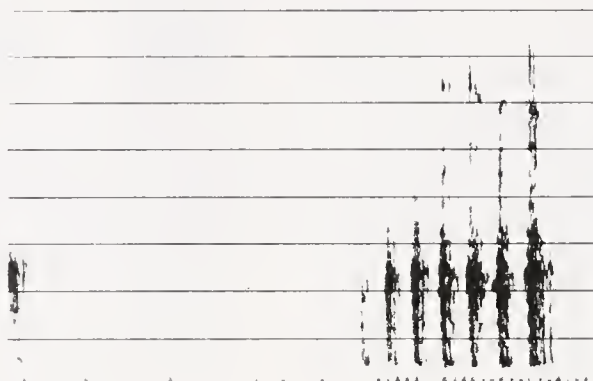
Their fundamental frequencies are approximately identical (0.5 kHz). Since fundamental frequencies are dependent on the oscillations resulting from air passing over the vocal cord, causing it to vibrate at a frequency which is a function of the mass and tension of the cord (Duellman and Trueb 1986), it is likely that the frogs have a common vocal structure.

As well as multi-note calls, *Rana nigromaculata* has a single-note call. Frogs in northern and central China (Beijing and Wuhan) emit this sound repeatedly and usually in groups. Each group is composed of 5-10 single-note calls. In Hongya, the single-note call could rarely be heard. Because *R. nigromaculata* in Sichuan is peripheral in distribution, we believe that the call structure in northern and central China represent the basic structure, and that the Sichuan structure was derived from it.

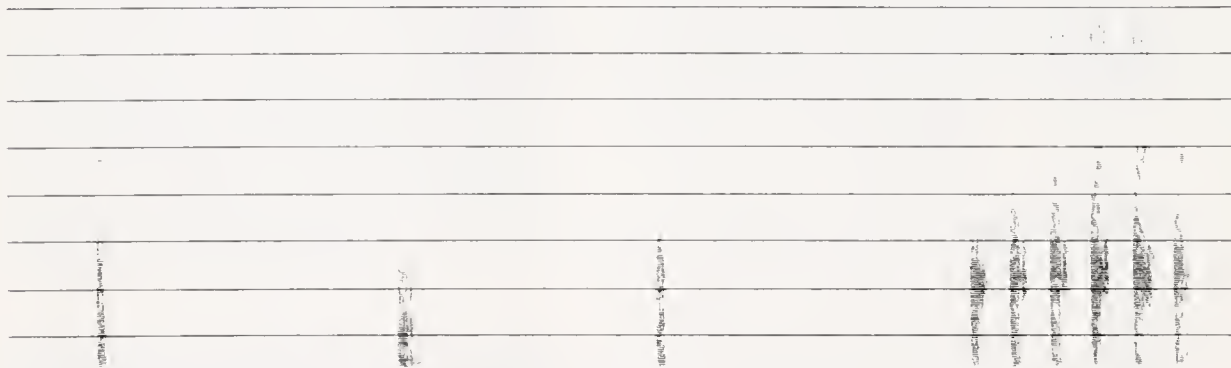
the divergence of call structure between northern and central China, and Sichuan. In comparing the three main acoustic parameters, call duration, pulse repetition rate, and mean dominant frequency, a general pattern is evident (Zweifel 1959). Pulse repetition rate and dominant frequency correlate positively with temperature, but duration of call correlates negatively with temperature. However, we feel that this is not sufficient to explain the differences between the populations. At a temperature only 3 and 5°C lower than in Wuhan and Beijing, respectively, the dominant frequency and pulse repetition rate of Sichuan *Rana nigromaculata* are about half of those found in the former localities. The length of calls of Sichuan frogs is approximately equal to the maximum call length of frogs from the Wuhan and Beijing localities, and their vocal sacs are of the same size. In addition, they have very similar fundamental frequencies. We conclude that they have nearly identical sound-producing

Table 1 and Figure 1 clearly demonstrate

TYPE B/65 SONAGRAM • KAY

a

TYPE B/65 SONAGRAM • KAY ELEMETRICS CO PINE BROOK, N.J.

b

TYPE B/65 SONAGRAM • KAY ELEMETRICS CO PINE BROOK, N.J.

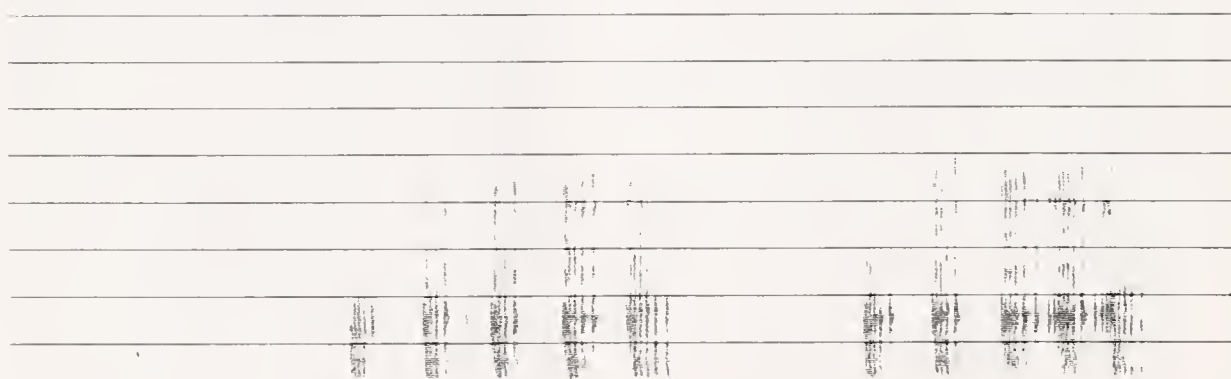
c

FIG. 1. Sonagrams of the calls of *Rana nigromaculata* in China. a. Seven note call from Beijing on May 27, 1988. The water temperature was 24°C. b. One 6 note call and two 1 note calls from Wuchang, Hubei Province, June 17, 1988. The water temperature was 22°C. c. Two 5 note calls from Hongya, Sichuan Province, March 19, 1988. The water temperature was 19°C.

structures, but different controlling mechanisms.

In acknowledging that our analysis of frog calls may not be exhaustive, we can only tentatively suggest that the Sichuan population of *Rana nigromaculata* is a separate subspecies from the Wuhan and Beijing populations.

Acknowledgments

We would like to thank Theodore J. Papenfuss (Museum of Vertebrate Zoology, University of California, Berkeley) for donating the sonograph paper, and Mitsuru Kuramoto of the Fukuoka University of Education, Japan.

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Four Remarkable Reptiles from South China Sea Islands, Hong Kong Territory

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Key Words: Reptilia, Squamata, Hong Kong, distribution.

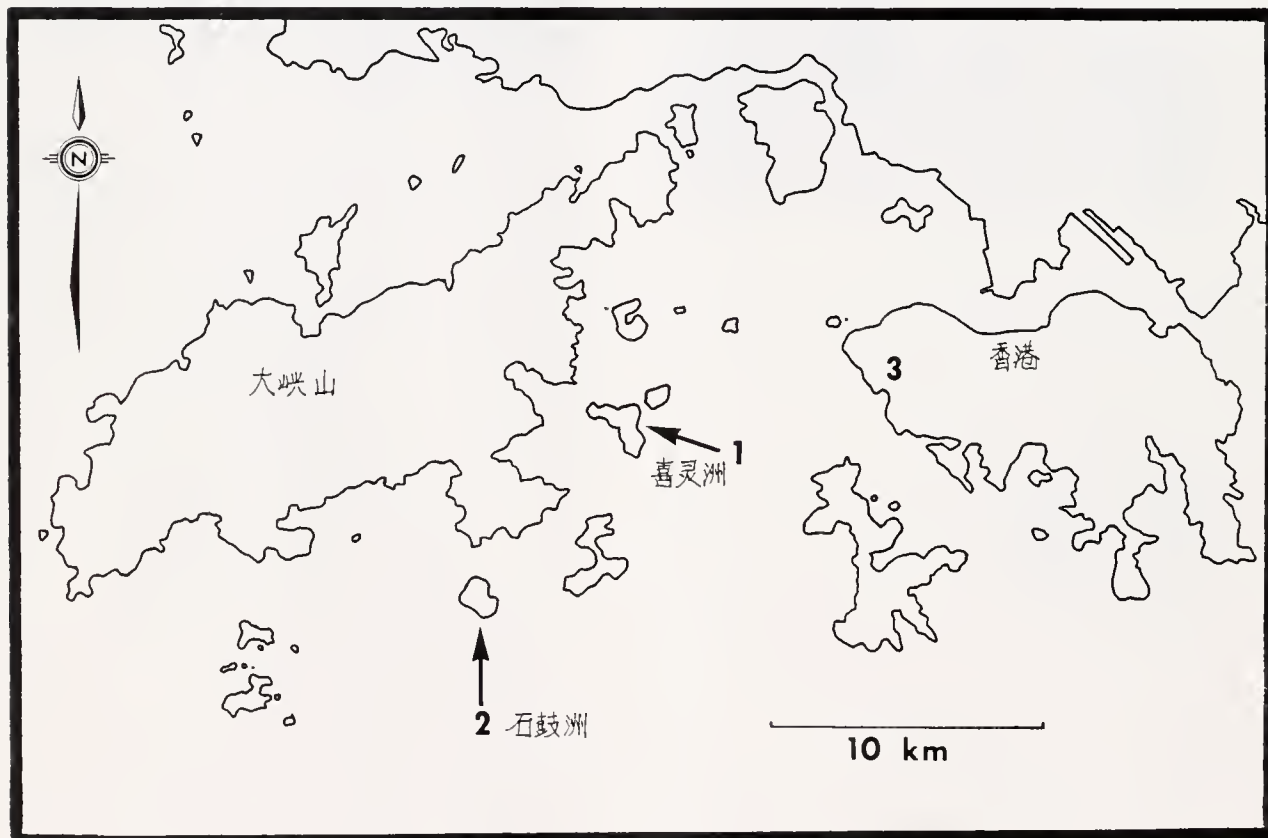


FIG. 1. Hong Kong and nearby islands. 1. Hei Ling Chau. 2. Shek Kwu Chau. 3. High West Pokfulam, Hong Kong Island.

Introduction

There are at least one hundred vegetated islands, presumably supporting amphibians and/or reptiles, within the Hong Kong Territory. This is estimated to be about three percent of the total number of continental shelf islands in the South China Sea between Taiwan and Hainan Dao. Nevertheless, the number of endemic and isolated species documented from the territory in the comprehensive work of Karsen, Lau, and Bogadek (1986) is high:

four endemics and at least fifteen widely disjunct populations. Here we add two species not previously recorded (both widely disjunct) and new records of species poorly documented before (Fig. 1). Voucher specimens are in the Museum of Comparative Zoology (MCZ), Harvard University.

Dibamus cf. *bourreti*
(White-tailed Two-footed Lizard)

A single specimen, MCZ 172041, was

collected by Anthony Bogadek, 1 April 1987, on Hei Ling Chau *ca.* 10 km southwest of Victoria, Hong Kong—a range extension northeast for the genus, and family Dibamidae of *ca.* 800 km (Lazell 1988).

The specimen, a 177 mm SVL male, was sent to Allen Greer, Australian Museum, Sydney, for identification. He believed the specimen was "probably" *Dibamus bourreti* (in litt., 9 May 1988). However, we note the following sharp distinctions from *D. bourreti* as diagnosed and described by Greer (1985: 148): the rostral suture is not complete, not present from lip to nostril but only posterior to the nostril. There is a prominent labial suture. There are no preanal or tibial pores. *Dibamis bourreti* is diagnosed as having a complete rostral suture, no labial suture, and four preanal pores on each side, even in a female—the highest count in *Dibamus*.

This specimen, MCZ 172041, has 23 scale rows at midbody, six scales fronting the hindlimb where Greer (1985:120) shows *D. novaeguinae* having four, and six rows of preanal scales where Greer (1985:120) shows *D. novaeguinae* having three. The hindlimb is 2.7% of SVL. The tail is 22.6% of SVL. In life this specimen was lilac of lavender-gray shading to buff on the head and chalk-white on the tail. It is much paler and less contrastingly marked than the Guangxi *D. bourreti* illustrated by Tian and Jiang (1986). See Figure 2.

Typhlops albiceps

This tiny snake, apparently rare throughout its range, was known from Hong Kong Island only on the basis of two specimens collected in 1959 and 1966 (Karlsen et al. 1986), now in the British Museum (Natural History): BMNH 1954.1.13.4 and BMNH 1983.946, respectively. It was rediscovered 27 May 1988 at High West, Pokfulam, Hong Kong Island by Sandra Brown (Macklin 1988). The species appears reasonably common at this site. Voucher specimens are at the St. Louis School, West Point, Hong Kong (curated by Anthony Bogadek) and at MCZ

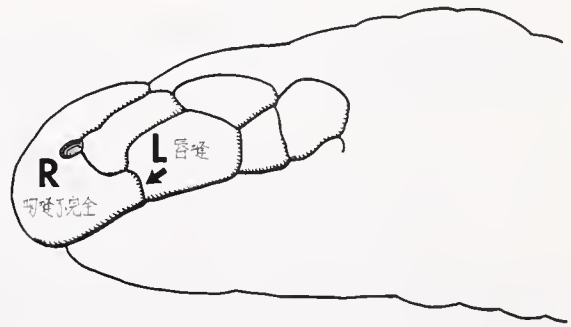


FIG. 2. *Dibamus* sp. from Hei Ling Chau. The rostral, R, lacks a suture from lip to nostril. A labial suture, L, is present.

(MCZ 173290).

Lance (1976) did not recognize "*Typhlina*" or "*Ramphotyphlops*" and neither do we. The putative distinction from *Typhlops* is entirely in male genitalia (McDowell 1974). Because females are indistinguishable, recognition of "*Typhlina*" or "*Ramphotyphlops*" directly violates the principles of systematic zoology (Mayr et al. 1953) and the principles of animal taxonomy (Simpson 1961).

This is the only species of *Typhlops* in China with 18 scale rows. It is very slender, the head spatulate. MCZ 173290 is 155.5 mm SVL with a 2.5 mm tail. The dorsum is wood brown shading to buff on the head. The chin is near-white; this color extends posteriorly for 10 scales onto the throat. The tail tip is near-white; this color extends anteroventrally on all 10 subcaudal scales and 4 rows anterior to the vent.

Dendrelaphis pictus (Painted Bronze Back Snake)

This elegant snake is known from Guangdong, Guangxi, and Yunnan (Hu et al. 1980), and from Hong Kong on the basis of a single report (Wall 1903). One of us (Lazell) has searched both BMNH and MCZ for this specimen with no success. Peaker (1987) criticized Karsen et al. (1986) for including this species in the Hong Kong fauna. Deletion would have

TABLE 1. Some scale counts for Chinese *Ahaetulla prasina*.

	Mainland	Shek Kwu Chau
Ventrals, males	186-209	217
Ventrals, females	191-204	224
Subcaudals, males	155-177	—
Subcaudals, females	150-169	184

been premature. Between 1971 and 1984 Dr. Barry Hollinrake, resident of Shek Kwu Chau, a small island 1.3 km south of Lanau, amassed a collection of 35 snakes on the island of 9 species, now housed at MCZ (Boalch 1988). Among these is a beautiful female *Dendrelaphis pictus* with 15 dorsal scale rows, 171 ventrals, and 131 subcaudals: MCZ 173278.

The ventral and subcaudal counts of the Shek Kwu Chau specimen are significantly lower than those given by Hu et al. (1980: 39): 184 ventrals (females 186-193) and 141-169 subcaudals (females 141-169).

Ahaetulla prasina (Jade Vine Snake)

Two specimens of this spectacular snake, never previously recorded in Hong Kong Territory, are in the Hollinrake collection from Shek Kwu Chau: male, MCZ 173303, and female, MCZ 173304. Their scale counts are much higher than those given by Pope (1935) of Hu et al. (1980) for this widespread South China species: Table 1.

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On the Independence of the Colchis Center of Amphibian and Reptile Speciation

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Abstract. -The Colchis region of Western Transcaucasia is characterized by a rather uniform thermal regimen, corresponding to a subtropical climate. The Colchis forests contain an extraordinary abundance and diversity of tree, shrub, and vine species. The herpetofauna of the Colchis forests is surprisingly poor, despite its uniqueness.

Key Words: Amphibia, Reptilia, USSR, Caucasus, biogeography.

Introduction

The herpetofauna of Western Transcaucasia is not homogeneous, due to the different age and genesis of the species distributions. Along with autochthonous and endemic forms, one can find species whose main areas of distribution are in the European part of the USSR and in the Eastern Mediterranean. At the same time, a number of species which have main distributional centers in the Colchis occur beyond the bounds of Western Transcaucasia, in other parts of the Caucasian Isthmus. For these reasons, it is necessary to define the Colchis herpetofauna and to determine its place in the fauna of reptiles and amphibians of the Caucasian Isthmus as a whole.

Research on this issue started with the works of Nordmann (1840), Derjugin (1899), Silant'ev (1903), Brauner (1905), and Nesterov (1911). However, the first well-grounded definition of the fauna in question from a zoogeographical point of view was presented in the works of Satunin (1912). Satunin wrote in 1910, "So far I cannot say much about the genesis of the fauna of this region called Western Transcaucasia. This country with its evergreen plants and scanty fauna resembles a piece of the Mediterranean in the narrow sense of the word. True, here are endemic species and forms, but not a single genus of vertebrate is unrepresented in the countries of the Mediterranean.

Often they are inhabited by the same species. The question is whether this fauna has appeared from the west or is it the remainder of the fauna that has populated densely the shores of the Black Sea at one time. It is impossible to answer these questions at the present level of our knowledge. But even now I can definitely say that this fauna by its origin, has nothing in common with the faunas in other regions of the Caucasus."

In 1912, Satunin divided the Caucasian Isthmus into five subregions and 11 districts, including the Colchis in the West-Transcaucasian district of the Littoral subregion.

Among other merits of this work by Satunin, one cannot but mention the fact that for the first time, he defined in an exact way the Colchis region proper. He defined the northern border as the spurs of the Main Caucasian Range up to the basin of the Tuapse River, the southern border as the Pontic Range, and the eastern border as the Arsijanskij Range. The valley of the Rioni River and the adjacent southern slopes of the Main Range were defined as the central part of the region. Satunin emphasized the depauperate herpetofauna of this region on one hand, and the presence of endemic species such as *Vipera kaznakovi* and *Bufo verrucosissimus* on the other hand.

Nikolsky (1911) assigned the entire Caucasus, excluding eastern Precaucasia,

to the Mediterranean. However, he could not differentiate the forest and the alpine belts of the Greater Caucasus, because of the absence of data.

Results and Discussion

Investigations of the last decades made it possible to add the majority of the species of the Colchis herpetofauna to an overall picture of Colchis faunal distributions (Turov 1928; Bartenev and Reznikova 1935; Khozatsky 1941; Milyanovskiy 1957; Bannikov et al. 1977; Negmedzyanov and Bakradze 1977; Orlova 1973, 1978a, 1978b; Golubev 1980, 1985; Tuniyev 1983, 1985). In addition there has been a revision of the taxonomic status of such forms as *Vipera kaznakowi* (Vedmederja et al. 1986; Orlov and Tuniyev 1986a, 1990 this volume), *Lacerta agilis* (Peters 1960), *L. derjugini* (Bartenev and Reznikova 1931; Orlova 1978a; Bischoff 1982, 1984), *L. saxicola* (Darevsky 1967; Darevsky and Vedmederja 1977), *Anguis fragilis colchicus* (Lukina 1965; Scherbak and Scherban 1980), and others.

Accumulation of this information along with works on fossil amphibians and reptiles of the Caucasus (Vekua et al. 1979; Chkhikvadze 1981, 1983, 1984; Bakradze and Chkhikvadze 1977; Zerova and Chkhikvadze 1984; Yefimov and Chkhikvadze 1987) have made it possible to revise the zoogeography of the region.

Darevsky (1957) singled out seven different groups of species and subspecies of the herpetofauna in the Caucasus, based on their origin. Among the species representatives of the region of interest to us, it is necessary to pay attention to *Lacerta strigata* (Asia Minor species), *Emys orbicularis*, *Anguis fragilis*, *Coronella austriaca*, *Elaphe quatuorlineates sauromates*, *Natrix natrix* (European boreal species), *Testudo graeca*, *Natrix tessellata* (Mediterranean species), *Pseudopus apodus*, *Coluber najadum* (east-Mediterranean species), and *Lacerta saxicola*, *L. praticola*, *L. derjugini*, *L. media* (autochthonous species). The

Colchis, however, was not distinguished as an independent center of speciation in this work.

Scherbak (1981) included the Colchis in the Caucasian Region of the Mediterranean Province. He suggested that the typical species of the region were *Mertensiella caucasica*, *Pelodytes causicus*, *Lacerta saxicola*-complex and others. However, the Colchis proper was again not distinguished as an independent center of herpetofaunal formation.

For the analysis of the herpetofauna of the Colchis proper, it is necessary to exactly define the term "the Colchis phytolandscapes", and to decide what types of vegetation are universally recognized as "Colchis types". Albov (1885) was the first to clearly depict plant landscapes of the Colchis. He singled out a region, unique for Russia, of mountain limestone flora which had been developing mainly autochthonously in a large refugium with numerous endemic and relict species and even genera. Kolakovskiy (1980) regarded the Colchis flora as basically forest and alpine-meadow, and suggested that its main phytolandscapes had existed since old times with changes only in the composition of their edificators, except for the extinct formation of evergreen subtropical forests in the lower mountain belt. The tertiary-relict character of the forest mesophile flora and vegetation is fully revealed here due to slight changes in this region's climatic conditions (Kuznetsov 1891). The most characteristic features of the tertiary-relict Colchis forest are: extraordinary abundance and diversity of tree and shrub species, impossibility of singling out the dominant species (which is also characteristic of tropical forest with extreme density of trees), abundance of vines and epiphytes, and almost total absence of grass cover. All these attributes make the Colchis forest similar in many aspects to a tropical rain forest (Pavlov 1984). According to Sinskaya (1933), the Colchis forest vegetation underwent three main stages of development: the tropical forest; the forest of Colchis type, but rich and covering a wider area; and last, the modern Colchis

forest.

The Colchis type of vegetation includes a number of phytocenoses differing in structure, composition, and ecological peculiarities: it may be mixed (polydominant), or may be presented by cenosis of one or two species, but the common and obligatory attribute of phytocenosis of the Colchis type is an abundance of tertiary relicts. The area with Colchis type vegetation is characterized by a rather monotonous thermal regimen, corresponding to a subtropical climate, but with highly diverse soils (Gulisashvili et al. 1975).

The herpetofauna of the Colchis forests is surprisingly poor, despite its uniqueness. The species composition is different in the southeastern and northwestern parts of the Colchis compared to the other portions of its territory. Species such as *Mertensiella caucasica*, *Lacerta clarkorum*, *L. parvula*, and *L. mixta*, whose distributions are connected with forests growing on acid soils above volcanic rocks, are found on the western slopes of the Adzharo-Imeretinsky, Shavshetsky and Lazistansky (Pontic) mountain ranges. Similarly, floristic endemics of this part of the Colchis (*Rhododendron unguernii*, *Osmanthus decorus*, *Betula medwedewii*, *Epigaea gaultheriodes*, and others), are Adzharo-Lazistan endemics, sometimes with slight radiations to the adjoining regions, but are not Colchis endemics in the broad sense of the word. The same applies to *Lacerta saxicola darevskii* and *L. saxicola brauneri* which are widespread in the northwestern part of the Colchis, but are absent in the central and southeastern Colchis. These animals, by analogy with floristic endemics (*Allium candolleianum*, *Campanula mirabilis*, *C. bzybica*, *C. calcarea*, *C. jadvigae*, *Genista abchasica*, *Gentiana paradoxa*, *Omphalodes kusnetzovii*, and others) are northern-Colchis endemics. For example, of the 450 endemic Colchis species of flora, 83 (25%) are endemics of the northern Colchis (Adzinba 1980). *Triturus vittatus ophryticus*, *T. vulgaris lantzi*, *Bufo verrucosissimus*, *Pelodytes caucasicus*, *Lacerta derjugini*, *L. agilis*

grusinica, *Natrix megalocephala*, and *Vipera kaznakowi* are Colchis endemics in the broad sense of the word.

In addition to the Colchis endemics, there are three more ecological-geographical groups of amphibians and reptiles in the region. They have similar ecological characteristics (habitat first of all), and overlapping geographic distributions.

1. The East-Mediterranean group consists of *Triturus cristatus karelini*, *Testudo graeca nikolskii* (Fig. 1), *Lacerta media*, *L. praticola pontica*, *L. strigata*, *Pseudopus apodus tracijs*, *Natrix tessellata*, and *Coluber najadum*. This group's distribution includes either the Balkans and the Caucasus or the Balkans, Crimea, and the Caucasus. According to ecological characteristics, these are xeromesophiles or hemixerophiles whose spreading is related to dry foothills of Western Transcaucasia up to 200-300 m above sea level with an annual sum of temperatures exceeding 5000°C. Thus, *Testudo graeca*, *Pseudopus apodus*, and *Coluber najadum* occur in the Colchis on a narrow seaside strip of land with enclaves of Mediterranean vegetation from Tuapse to Pitsunda-Sukhumi. A local population of *L. strigata* occurs in the Pitsunda region, and a local population of *L. media* occurs in the environs of Pitsunda and Salme. The majority of localities of *L. praticola* and *Natrix tessellata* in the Colchis are in the seaside hills up to 400 m above sea level. It is only along the valleys of large rivers like the Shakhe River, the Mzymta River, the Bzyb River, and others that *N. tessellata* penetrates into the Colchis up to 600 m above sea level. Thus the majority of these species are found either in places with vegetation of the Mediterranean type, or in places where the initial Colchis vegetation has been reduced to zero and the landscapes resemble the Mediterranean ones by their thermo-biotope conditions (substitute shibliaks and tomillares, Pitsunda pine groves, foothill post-forest glades, and landplots with *Erica tetralix*, *Juniperus oxicedrus*, *Pinus pitysusa*, and *Arbutus andrachne*).



FIG. 1. *Testudo graeca nikolskii* is a Mediterranean species, and in the Colchis it is found only in the seaside strip of land with enclaves of Mediterranean vegetation.

2. The Caucasian group includes *Hyla arborea schelkownikowi* (Fig. 2), *Rana macrocnemis*, *Lacerta caucasica alpina*, *L. rudis*, and *Vipera dinniki*. Distributions of these species in the Caucasian Isthmus are broader than those of the Colchis group. At the same time, the majority of them are Colchis autochthons. These species are mesophiles and occur in mesophillous forest and mountain meadow formations. This group seems to be of Colchis origin, retaining close connections with the main center of the formation. Broader ecological tolerance in comparison with typical Colchis species makes it impossible to include them within the Colchis group.

3. The European group consists of *Bufo viridis*, *Rana ridibunda*, *Emys orbicularis*, *Anguis fragilis*, *Natrix natrix*, *Coronella austriaca*, and *Coluber jugularis caspius*.

The composition of this group is not homogeneous. It includes both species typical for the steppe areas (*Bufo viridis* and *Coluber jugularis*) and those that are widely distributed in Europe (all the rest). Only *Anguis fragilis* and *Coronella austriaca* are widely distributed in the Colchis. This makes it difficult to definitely consider them late migrants to the Caucasus. Other species either occur in several spots along the Colchis seashore (*B. viridis* and *Natrix natrix*) or populate a narrow strip of land along the sea together with the Mediterranean species (*C. jugularis*) or a somewhat wider strip (*Emys orbicularis* and *Rana ridibunda*). Despite the possibility of finding these species in the typical Colchis forest formations, the majority of them are still attributed to the Mediterranean type of vegetation.



FIG. 2. *Hyla arborea schelkownikowi* seems to be of a Colchis origin, but because of its broad ecological tolerance, it is found in a large part of the Caucasian Isthmus.

Let us consider the dispersal and distribution of the representatives of the Colchis group in detail. *Triturus vittatus* occurs in the territory from the seashore to the subalpine meadows in all the forest types. In the place called "the Colchis Gates" (lowering of the Main Caucasian Range between Mt. Fisht and Mt. Chugush) the species crosses over to the northern slope of the Western Caucasus, reaching the environs of Goriachij Klutch and Krasnodar in the northwest and the basin of the Laba River in the northeast. In the eastern part of the area, the species crosses the Adzharo-Imeretinskij mountain range and reaches the outskirts of Tbilissi-Oni. It occurs in the Lagodekhi region as an isolate. Outside the boundaries of the Colchis this species occurs either in the Colchis type forests or in their derivatives.

Triturus vulgaris lantzi (Fig. 3) occurs in the same places in the Colchis as *T. vittatus ophryticus* does. Very often both species are symbiotopic (Tuniyev and Beregovaya 1986). On the northern slope of the Western Caucasus, its home range is wider than that of the previous species, but it is only through the mesophillous forests and subalpine meadows that it penetrates into the Eastern Transcaucasia up to the Trialet Ridge. The isolated population in Talysh occurs in the Hirkan forests which are ecologically and genetically close to the Colchis forests.

Bufo verrucosissimus (Fig. 4) occurs in all parts of the Colchis from the sea shore up to the subalpine forests. On the northern slope of the Western Caucasus, it is found on the territory from the environs



FIG. 3. *Triturus vulgaris lantzi*. This subspecies is widespread throughout the Colchis.

of Krasnodar in the west to the Psebj settlement and the Shakhgirej Canyon in the east, where it is found in the derivatives of the Colchis forests from 400 m to 1000 m above sea level. In the Eastern Caucasus it is found in the Borzhomy Gorge, the Lagodekhi-Zakataly, and the Talysh region, where its distribution is limited to the mesophilous forests, which are abundant in the Colchis and Hirkan floral elements.

The distribution of *Pelodytes caucasicus* (Fig. 5) in the Colchis is more restricted. It does not occur in the coastal belt and oak-forests. It is found both in the mesophilous beech, chestnut, and fir-tree forests, and in mixed broad-leaved forests with an evergreen understory. On the northern slope of the Western Caucasus, its distribution coincides with that of *B. verrucosissimus*, but unlike the latter, it is not found in deforested places. Its

southeastern distributional limits also coincide with that of *Bufo verrucosissimus*. *Pelodytes caucasicus* does not occur east of the Trialet Ridge. There is an isolated population in the mesophilous forests in the Lagodekhi-Zakataly region.

Lacerta derjugini has a distribution in the Colchis similar to *P. caucasicus*. It reaches the sub-alpine belt. On the northern slope of the Western Caucasus, it is found in the Colchis forest derivatives from the Belaja River to the Small Laba River (the Shakhgirej Gorge). The species penetrates through the Eastern Transcaucasia up to the Trialet Ridge. Separate populations occur in north-eastern Georgia up to Lagodekhi-Zakataly.

Lacerta agilis grusinica (Fig. 6) is known to occur only on the territory of the Colchis and the adjoining sea coast up to



FIG. 4. *Bufo verrucosissimus*. This Colchis endemic occurs in the four Colchis refugia.

Novorossiysk. Its vertical distributional limit is 700 m above sea level, though local populations can be found in the sub-alpine belt (Mt. Aishkho and Mt. Uglovoj).

The distribution of *Natrix megalcephala* is similar to that of many Colchis species. It is found from the environs of Tuapse and Gorjachij Kljutch in the west, to the region between the Belaja Laba River and the Small Laba River in the north, eastwards through the whole territory of the Colchis up to the Borzhomy Gorge and separately in the Lagodekhi-Zakataly region (Orlov and Tuniyev 1986b). In the Colchis it reaches the sub-alpine belt. In the rest of the area it does not exceed 1000 m above sea level.

Elaphe longissima (Fig. 7) occurs in the region of Novorossiysk and throughout Western Transcaucasia, except for the mid-

mountains and highlands. There are isolated populations in the Borzhomy Gorge, the Lagodekhi-Zakataly region and the Belaja River basin on the northern slope of the Western Caucasus.

Vipera kaznakowi (Fig. 8) occurs throughout the territory of the Colchis up to 1000 m above sea level. On the northern slope of the Western Caucasus it occurs between the Belaja River and the Small Laba River. Separate populations are known in the Borzhomy Gorge and the Lagodekhi region.

The dispersal and distribution of *Lacerta saxicola darevskii* (Fig. 9), *L. s. brauneri*, *L. mixta*, *L. parvula* and *Mertensiella caucasica* have been analyzed above.

A comparison of the endemic Colchis species, whose distributions are associated



FIG. 5. *Pelodytes caucasicus* occurs in all four Colchis refugia.

with forest and meadow formations of the Colchis type, makes it possible to identify three more regions in the Caucasian Isthmus, besides the Western Caucasus (the Colchis proper), in which the Colchis herpetofauna occurs. The three regions are: the Bjelo-Labinskij region on the northern slope of the Western Caucasus, the Kakhetinskij (Lagodekhi-Zakataly) region on the southern slope of the Eastern Caucasus, and the Borzhomskij region in Eastern Transcaucasia (Fig. 10). The comparative composition of the herpetofauna of these regions is shown in Table 1.

It is evident from Table 1, that the most significant differences are found between the Colchis and the Kakhetinskij regions and the least significant differences are between the Colchis and the Borzhomskij and the Belo-Labinskij regions. Taking into

account the above mentioned peculiarities of distribution of herpetofauna within the Colchis refugium itself, the differences become even less significant. In this case, we deal with three regions smaller in space, and a wealth of species of the Colchis herpetofauna that occur in refugia and have survived off the main territory of the Colchis.

The Belo-Labinskij region is only conventionally separated from the Colchis by the crest of the Main Caucasian Mountain Range. All the northern Colchis species, except *L. a. grusinica*, occur on the northern slope of the Western Caucasus in the Belaja and the Small Laba river drainages. It should be stressed that this unity is based on the fact that the characteristic Colchis elements of flora and vegetation cross over the Main Caucasian Range in the place known as "the Colchis Gates" to its northern slope. The basins of



FIG. 6. *Lacerta agilis grusinica* is found throughout the main Colchis refugium.

TABLE 1. Distribution of the endemic Colchis herpetofauna in the main refugia of the Caucasian Isthmus.

Species	R Colchis	E Bjelo- Labinskij	G I Kakhetinskij	O N Borzhomskij
<i>Triturus vittatus</i>	+	+	+	+
<i>T. vulgaris lantzi</i>	+	+	-	+
<i>Mertensiella caucasica</i>	+	-	-	+
<i>Bufo verrucosissimus</i>	+	+	+	+
<i>Pelodytes caucasicus</i>	+	+	+	+
<i>Lacerta derjugini</i>	+	+	+	+
<i>L. agilis grusinica</i>	+	-	-	-
<i>L. saxicola darevskii</i>	+	+	-	-
<i>L. s. brauneri</i>	+	+	-	-
<i>L. mixta</i>	+	-	-	+
<i>L. parvula</i>	+	-	-	+
<i>L. clarkorum</i>	+	-	-	-
<i>Natrix megalcephala</i>	+	+	+	+
<i>Elaphe longissima</i>	+	+	+	+
<i>Vipera kaznakowi</i>	+	+	+	+
Total:	15	10	7	11



FIG. 7. *Elaphe longissima*. The Colchis refugia populations are disjunct from the main distribution in Europe.

the Belaja, Tsitse and Laba rivers abound in those elements. To the north of these watersheds their distributions are continuous up to the Skalistij (Rocky) limestone ridge. Maleyev (1939) has noted that a part of the Maikop district abounds in Colchis elements and is inseparable from the Colchis according to the character of its flora and vegetation.

The Borzhomskij region is also conventionally separated from the Colchis by the Adzhara-Imeretinskij Mountain Ridge. The flora and vegetation of the Baniskhevskoje Gorge, the Likanskoje Gorge, and the upper belt of Mt. Lomis-Mta, as well as the environs of Bakuriani, hardly differ from those of the Colchis.



FIG. 8. *Vipera kaznakowi* occurs throughout the territory of the Colchis up to 1000 m above sea level.

In the isolated eastern Kakhetinskij region a considerable number of the ancient Tertiary vegetation representatives survived due to the warm and humid climate (Gulisashvili et al. 1975).

Modern distributions of eco-geographic groups of amphibians and reptiles distinguished by our scientists have distinct altitudinal-ecological limits owing to natural and historical reasons.

Migration of ancestral species of the Colchis and the Caucasian groups from the south apparently took place in the Miocene when the Caucasian island joined vast territories of Asia Minor. Colonization of the Caucasus from the south by different species of mammals during the early Miocene has been studied by Vereschagin (1958), and that of lizards of the *Podarchis-Archaeolacerta* group by Darevsky (1967).

The early Miocene was about the time of the formation of the Caucasian Mountains (Bogachev 1938).

The warm subtropical climate and vegetation in the Caucasus favored the evolution and dispersal of heat and mesophilic forms (*Triturus vittatus ophryticus*, *T. vulgaris lantzi*, *Pelodytes caucasicus*, *Bufo verrucosissimus*, *Lacerta saxicola darevskii*, *L. s. brauneri*, *L. derjugini*, *Elaphe longissima*, *Natrix megalcephala*, and *Vipera kaznakowi*), as well as species with a broader ecological tolerance (*Rana macrocnemis*, *Hyla arborea schelkownikowi*, *Lacerta rudis*, and *L. agilis grusinica*).

Fossil remains of mammals (*Mesocricetus*, *Prometheomys*, *Sorex*, *Talpa*) [Vereschagin 1958] and insects (Orthoptera, Hemiptera, Blattoidea, and



FIG. 9. *Lacerta saxicola darevskii*. This lizard is a Colchis endemic whose distribution is restricted to the northwestern part of the Colchis.

Coleoptera) [Rodendorf 1939] suggest a good food supply for amphibians and reptiles during the Miocene. It was also in the Miocene that the majority of these species reached the eastern-most parts of the Greater Caucasian Range along its southern slopes and penetrated from there into the Talysh across the so-called "Karabakhi Bridge". Safarov (1966), and other scientists, have studied the former direct relations between the Colchis and the Hirkan floras. Even at the present time, the floristic composition of the Kakhetinskij region and of the Karabakh has many common features with that of the Colchis and the Talysh forests (Arushanyan 1973; Sokolov 1977; Takhtadzhan 1978; Gadzhiev et al. 1985).

The end of the Tertiary period was characterized by damping of tectonics due

to the broad correlation of the Caucasus and the Balkans (Vereschagin 1958) and the formation of the steppe landscapes along the northern Black Sea coast (Pidoplichko 1954; Scherbak 1966). During that period, such South-European species as *Rana ridibunda*, *Bufo viridis*, *Emys orbicularis*, *Anguis fragilis*, *Coluber jugularis*, and *Coronella austriaca* seem to have penetrated to the Precaucasia from the west. At the same time, such species as *Testudo graeca*, *Pseudopus apodus*, *Triturus cristatus karelini*, *Lacerta praticola pontica*, *L. media*, *Coluber najadum*, and *Natrix tessellata* got into the Colchis from the west along the Black Sea coast.

Early and Middle Pliocene should be considered the beginning of initial fragmentation of the Colchis faunal areas when the Greater and the Lesser Caucasian

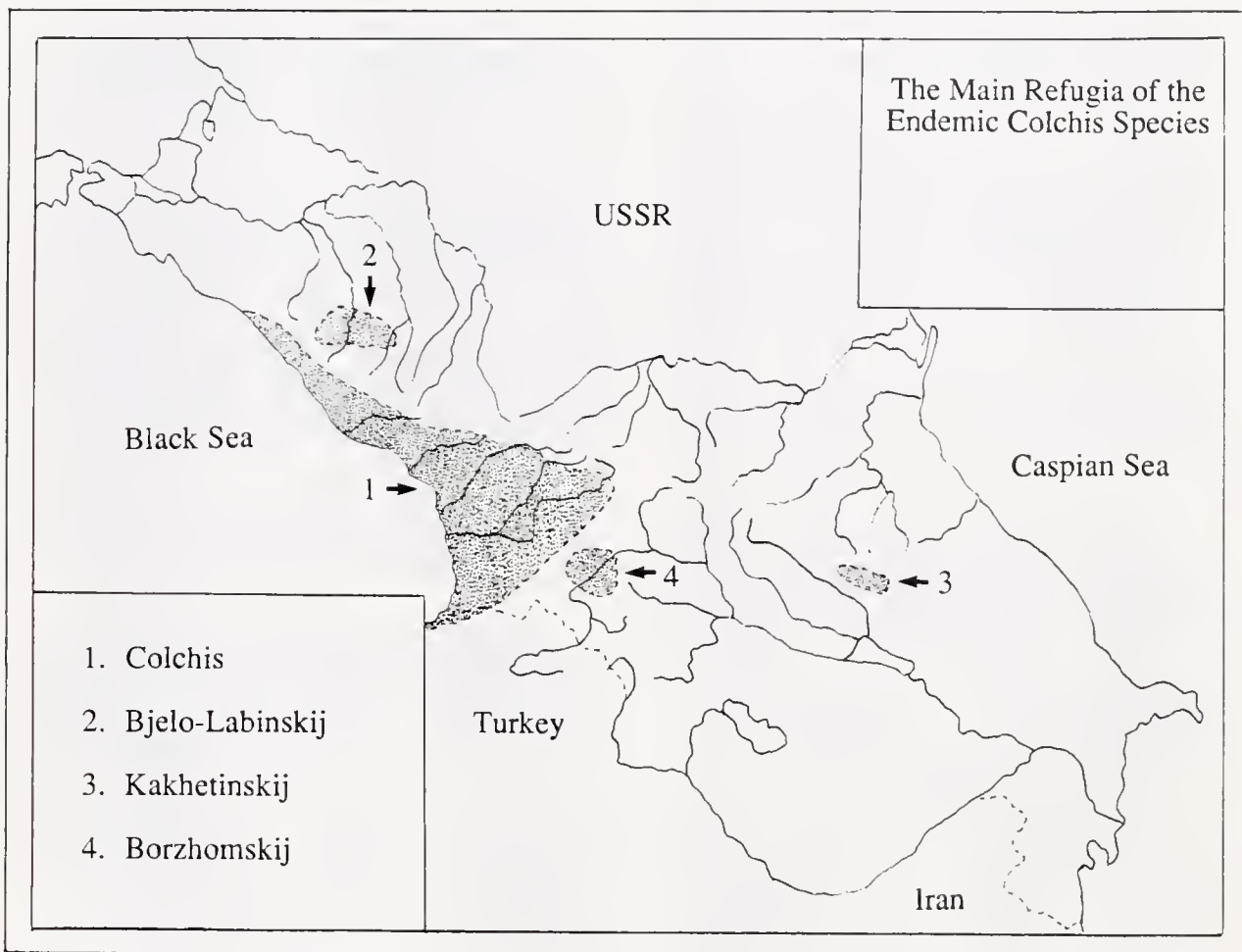


FIG. 10. The main refugia of the endemic Colchis herpetofauna.

Mountain ranges underwent substantial glaciation (Grozdetzkiy 1954; Markov et al. 1965). The main center of dispersal of these species was the Colchis, where relatively heat-loving vegetation of the Caucasian type survived even during the periods of the extreme Pleistocene cooling (Vereschagin 1958; Adamyants 1971). Along with the Colchis, smaller refugia sporadically survived on the territory of the Caucasus Black Sea coast, and also on the northern slope of the Main Caucasian Range between the Pshekha River and the Small Laba River. The present distribution of the Tertiary vegetation of the Colchis type in the western Caucasus testifies to this (Kharadze 1974; Pechorin and Lozovoy 1980; Kholyavko et al. 1978; Adamyants 1971; Koval and Litvinskaya

1986).

It was in the narrow humid gorges with a relatively constant thermal regimen that the representatives of the Colchis group remained intact. At the same time, independent populations might also have been preserved in mid-mountain areas where refugia of the Colchis vegetation exist in the vicinities of the Fisht-Oshtenskij Mountain Massive, the Lagonaki Plateau and even in the Central Caucasus (Kholyavko et al. 1978; Kharadze 1974). Small refugia seem to have also remained on the southern slope of the eastern part of the Greater Caucasus and in the Kuru River Gorge. It is indisputable that the majority of the mountainous populations of Colchis species perished during the Pleistocene and

that the ones that survived in refugia have been accumulating unique characteristics which led to different geographical forms (subspecies) on different slopes of the Main and the Adzharo-Imeretinskij mountain ranges. The data presented by Takhtadzhian (1946) and Maruashvili (1956) support the hypothesis concerning the preservation of relict Colchis species in the mountains. According to their data, the average annual temperature during the glacial periods decreased not more than 1.5-2.0°C, while precipitation amounted to not less than 1500-2000 mm.

Darevsky (1967) considers that this argument supports the possibility of foothill refugia of reptiles existing on the sea facing slopes of the Gagrinskij and the Bzhybskij mountain ranges, and in other regions, despite radical reorganization of the distributions of all the species of plants and animals in connection with glaciation.

During the interglacial and especially the postglacial periods, reconstruction of all vegetation belts took place (Vereschagin 1958). This favored the isolation of the species of the Colchis and the Caucasian groups in the above-mentioned refugia, but favored wider dispersal of the European and the Mediterranean groups in Transcaucasia. In the northwestern part of the Caucasus Black Sea coast, mesophilic vegetation gave way to xerophytic vegetation of the Mediterranean type. Plant formations of this type with the prevalence of *Juniperetum*, *Querceto*, *Pinetum carpinulosum*, *Pinetum fruticosum* and shibliaks are characteristic of the Anpa-Gelendzhik region. Enclaves of Mediterranean vegetation remained still further to the south, up to Pitsunda (Takhtadzhian 1978; Kolakovskiy 1961).

When the xerothermic period ended, the climate became more humid again. This favored the reestablishment of the former borders of the forest belt (Vereschagin 1958). Subalpine meadows and elfin woodlands were expanding throughout the whole subalpine belt of the southern slope of the Main Caucasian Mountain Range from the Central Caucasus to the Fisht-

Oshtenskij Mountain Massive (Kholyavko et al. 1978; Kharadze 1974; Dolukhanov 1974; Galushko 1974). On the northern slope such vegetation is present in the western parts and changes its character to the east, transforming into a steppe type (Lavrenko 1980). Modern areas of *Vipera dinniki* and *Lacerta caucasica alpina* have fixed distributional limits in the subalpine belt influenced by the warm Black Sea. Final settling of the present-day climate favored fixation of the Colchis species distributions, with their distinct populations exceeding the bounds of the refugia. This was coupled by simultaneous depression and reduction of the European and especially of the Mediterranean species distributions.

Concluding this review of the Colchis herpetofauna and their main refugia, it is necessary to enumerate the most important characteristics. The Colchis species are characterized by antiquity (conservation since the Tertiary period), Autochthony, depression—for some species (*Vipera kaznakovi*; *Lacerta clarcorum*, *L. a. grusinica*), existence of the northern-Colchis limestone, and the southern-Colchis volcanic centers of formation of narrow-endemic forms. Reptiles have a common tendency toward melanism, while amphibians approach their low temperature thresholds. These are the adaptive features acquired during the glacial period. As a rule, the modern distribution of the Colchis species does not exceed the bounds of the Colchis vegetation refugia or their derivatives.

The maximal vertical distribution is in the center of the Colchis up to 1800 m above sea level, while in the other portions of the refugia it does not exceed 1000 m above sea level as a rule. The existence of four refugia of the Colchis herpetofauna in the Caucasian Isthmus is determined by natural factors of high order—these are the areas with slightly changed climatic conditions characterized by modern crossing of the January -3°C isotherm and 800 mm isohyet.

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Studies of the Early Embryonic Development of *Rana rugulosa* Wiegmann

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Abstract. -This paper deals with the early embryonic developmental stages of *Rana rugulosa* Wiegmann, and with methods of artificial fertilization and experimentally accelerated development. Developmental stages are distinguished by morphological changes and obvious physiological features. At a temperature of 25.1 to 27°C it takes 70 hr 20 min to complete development from fertilized eggs to tadpoles with opercular folds. This course of development is divided into 25 stages, which are standardized with normal table equivalents.

Key Words: Amphibia, Anura, Ranidae, *Rana rugulosa*, embryonic development, artificial fertilization, accelerated development, fertilized eggs, normal table.

Introduction

Rana rugulosa Wiegmann, whose popular name is the Field Chicken in China, is strong and big of body. It is famous for its delicacy of meat and the price is dear. Domestic and foreign markets are in great need of it. The growth and development of these frogs are relatively quick. Hatchlings can become sexually mature in one year. The average body length is about 110 mm. The weight is about 0.25 kg. Consequently, *Rana rugulosa* farming has been a growing enterprise. More papers deal with the embryonic development of *R. guentheri* Boulenger and *R. catesbeiana*. Currently there are few domestic and foreign studies on the embryonic development of *R. rugulosa*. In order to produce reference material for the captive breeding of this frog, we studied its early embryonic development, using artificial fertilization and higher temperatures to accelerate development experimentally, during the months of April and June, 1987 and 1988.

Methods

We made 11 observations on the embryonic development of *Rana rugulosa*. Six of the 11 were artificially fertilized. The parent frogs were bought in Guangzhou. The description of the features of embryonic development was mainly based on the six artificially fertilized

eggs. The water temperature of the six developing embryos was 25.1 to 27°C; the pH was 6.5-6.8. Several minutes after oviposition and ejaculation or artificial fertilization, we put the oocyte into the laboratory. Then we used a microscope to observe the course of development and to measure the size and shape. The developmental stages were defined as beginning when half of the embryos in a sample showed all of the distinguishing characters of that stage.

For every developmental stage we took 10 to 20 embryos and fixed them in 5% formalin and Bouin's fluid. This material was used in drawings, tissue-slices, and photomicrographs. The figures shown here were taken from observations of living material.

Results

The 25 stages of the early embryonic of *Rana tigrina* are as follows (time in parentheses is hours and minutes after fertilization):

1) *Oocyte stage.* Unfertilized eggs are spheres 1.4-1.7 mm in diameter (Fig. 26). (00:25-00:30): The egg membrane absorbs water and expands. The eggs reach 2.6-4.0 mm in perivitelline space. (00:50): The pigment crown of the animal pole extends downward upon the gray crescent (Fig. 1a, 1b, 1c, 1d, 1e, 26).

- 2) *2 cell stage*. (01:12): The first longitudinal cleavage progresses and a cleavage furrow in the animal pole appears, forming 2 equal hemispheres (Fig. 2a, 2b, 27).
- 3) *4 cell stage*. (01:33): A cleavage furrow in the animal pole appears, perpendicular to the first cleavage furrow. It progresses to the vegetal pole and forms four equal sections (Fig. 3a, 3b, 28).
- 4) *8 cell stage*. (01:42): The third cleavage furrow appears parallel to the equator, approximately bisecting the animal hemisphere, forming four small animal cells and four large vegetal cells (Fig. 4a, 4b, 29).
- 5) *16 cell stage*. (01:48): Observed from the animal pole, the fourth cleavage forms eight blastomeres in two circular or elliptical tiers (Fig. 5a, 5b, 30).
- 6) *32 cell stage*. (02:05): The fifth cleavage is horizontal. The animal pole has eight small cells; the vegetal pole has 8 large cells (Fig. 6a, 6b, 31).
- 7) *Early blastula stage*. (02:23): The embryo is at the large cell blastula stage, but the cells are still clearly distinguished. The blastocoel begins to appear in the middle part of the embryo near the animal pole (Fig. 7a, 7b, 32).
- 8) *Mid-blastula stage*. (02:50): There are many small blastomeres. The blastocoel continues to amplify (Fig. 8a, 8b, 33).
- 9) *Late blastula stage*. (03:18): The blastomeres are the color of a red bayberry. The cell boundary becomes indistinct and the blastocoel expands to its maximum (Fig. 9a, 9b, 34).
- 10) *Early gastrula stage*. (05:56): The pigmented crown epiboly of the animal cap occurs, extending to cover over 75% of the embryo. The dorsal lip forms. Involution of cells begins (Fig. 10a, 10b, 35).
- 11) *Mid-gastrula stage*. (07:00): The dorsal lip continues to amplify. The cells on the side of the lip are drawn into the future archenteron and a semicircle appears (Fig. 11a, 11b, 36).
- 12) *Late gastrula stage*. (08:05): The blastopore shrinks and closes gradually. Eventually, the yolk plug is enclosed in the embryo (Fig. 12a, 12b, 12c, 12d, 37).
- 13) *Neural plate stage*. (10:30): The blastopore becomes a fissure, and the embryo begins to elongate along the longitudinal axis, becoming pear-shaped (Fig. 13a, 13b, 38).
- 14) *Neural fold stage stage*. (11:50): A fold appears on both sides of the neural plate. The neural groove forms the median sinus of the embryo. The front of the plate is bigger, and the neural fold gradually approaches the dorsal axis from both sides. The embryo elongates to 1.9 mm (Fig. 14a, 14b, 39).
- 15) *Cilial movement stage*. (12:40): The neural folds are joining. The embryo rotates within the vitelline membrane (Fig. 15a, 15b, 40).
- 16) *Nerve tube stage*. (13:45): The neural tube has formed and the gill plate and the cement gland can be seen (Fig. 16a, 16b, 41).
- 17) *Tail bud stage*. (14:55): Two outer gill buds protrude on the side of each gill plate. The total length is 3.0-3.6 mm, and the length of the tail bud is 1/10 to 1/7 of this (Fig. 17a, 17b, 17c, 42).
- 18) *Muscle effect stage*. (15:55): Muscular response begins in most individuals. The olfactory organ appears, the cement gland is complete. Total length is 3.3-3.8 mm., and the length of the tail bud is 1/7 of this (Fig. 18a, 18b, 18c, 43).
- 19) *Hatching stage*. (16:45): The embryo hatches from the egg membrane and two outer gill budlets with 3-5 branches protrude obviously (Fig. 19a, 19b, 19c, 19d, 44).
- 20) *Heart beat stage*. (29:25): The heart

begins to move, the eyes protrude, the pair of otoliths can be seen, and the 3rd external gill matures (Fig. 20a, 20b, 20c, 45).

21) *Open mouth stage.* (31:10): The membrane covering the mouth splits to show the mouth cavity. The alimentary canal is complete and body segments are obvious. The inverted "V" shape myomeres appear on the side of the embryo. Body length is 5.8-6.2 mm. Tail fin length is half of the body length (Fig. 21a, 21b, 21c, 46).

22) *Tail fin blood circulatory stage.* (32:00): The cement gland begins to degrade, circulation begins in the tail bud, and tadpoles are able to swim in a straight line (Fig. 22a, 22b, 22c, 47).

23) *Gill opercular fold stage.* (35:55): The opercular fold appears in the base of the external gill and the intestines form a bow (Fig. 23a, 23b, 23c, 48).

24) *Right side operculum closed stage.* (55:30): The opercular fold stretches toward the right side, the right external gill is covered and forms the right internal gill. The left external gill is exposed. The intestines have 2-3 twists. Total length is 6-9 mm (Fig. 24a, 24b, 24c, 49).

25) *Operculum completion stage.* (70:20): The external gill is entirely enclosed in the gill cavity, the posterior of which has an exhalent pore to the left side. The yolk has almost been absorbed, and the tadpoles begin feeding. Total length is 6.8-10.5 mm (Fig. 25a, 25b, 25c).

Table 1 shows N & F normal table equivalents (Nieuwkoop and Faber 1967) of our results.

Discussion

1. The circumstances of the early embryonic development of *Rana tigrina*, *R. catesbeiana*, *R. limnochiris*, and *R. nigromaculata* basically identical, but *R. rugulosa* has some minor differences in developmental timing.

TABLE 1. Normal table equivalents (Nieuwkoop and Faber 1967) of the developmental stages of *Rana rugulosa* as listed in this paper.

N & F stages	Pan & Liang Stages
1	1
2	2
3	3
4	4
5	5
6	6
7	7
8	8
9	9
10 ¹ / ₄	10
10 ¹ / ₂	11
11	12A
11 ¹ / ₂	12B
12	12C
12 ¹ / ₂	12D
13	13
15	14
17	15
21-22	16
24-25	17
29/30	18
33/34	19A
37/38	19D
39	20
40	21
41	22
42	23
45	24
47	25

2. During early embryonic development, we raised *Rana rugulosa* in water of about 25.1 to 27.1°C. It takes only 70 hr, 20 min to develop from oocyte to gill cover stage. Under the same conditions, *R. catesbeiana* is 60 to 70 hr slower, and *R. limnochiris* is 80 hr slower. Speed of development is closely related to temperature. At 26 to 28.5°C this developmental period in *R. rugulosa* takes only 64 hr, 30 min.

3. Fifty-five minutes after fertilization, the grey crescent of *Rana rugulosa* appears. This is identical to the timing of *R. catesbeiana*, but different from that of *R. nigromaculata*, in which the grey crescent can barely be seen, or is not visible.

4. The development of *Rana rugulosa* from the eight cell stage to the 16 cell stage takes six min, while the same period takes 59 min in *R. catesbeiana*.

5. In *Rana rugulosa*, external gill develops 3-5 branches during the period of hatching, while in *R. catesbeiana*, the external gill develops 2-3 branches during the tail bud circulatory stage. The third external gill appears sooner in *R. rugulosa* than in *R. catesbeiana* or *R. guentheri*.

6. Eggs laid by *Rana rugulosa* adhere in a pile or on the surface of the water. A reason for low hatching success is that oxygen levels can be low in the center of the egg mass. According to our observations, eggs at the edge of a mass are easy to hatch. If we separate the masses early enough, adequate dispersion can be achieved. However, the operation must be a careful one, or the egg membranes will be broken and the proper development of the embryo can be affected, causing deformity and death.

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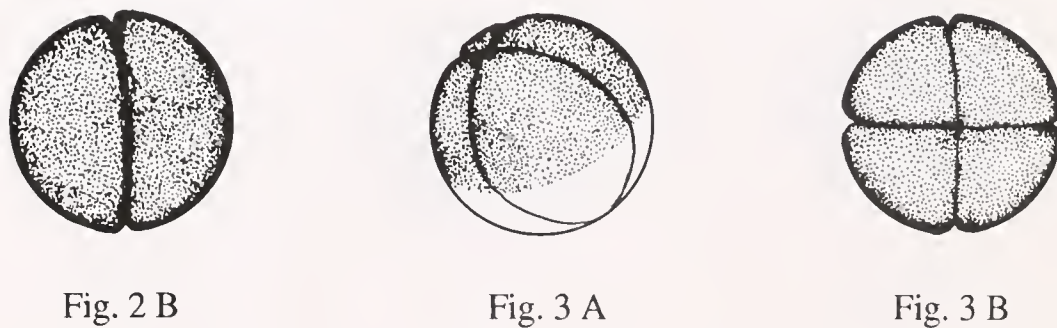
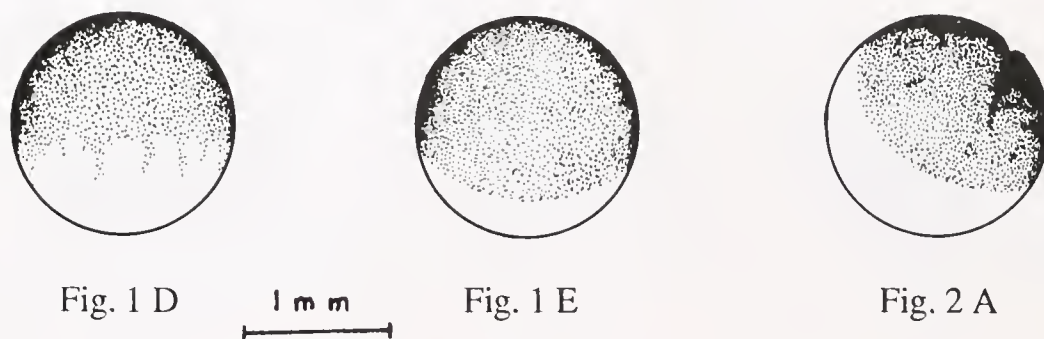
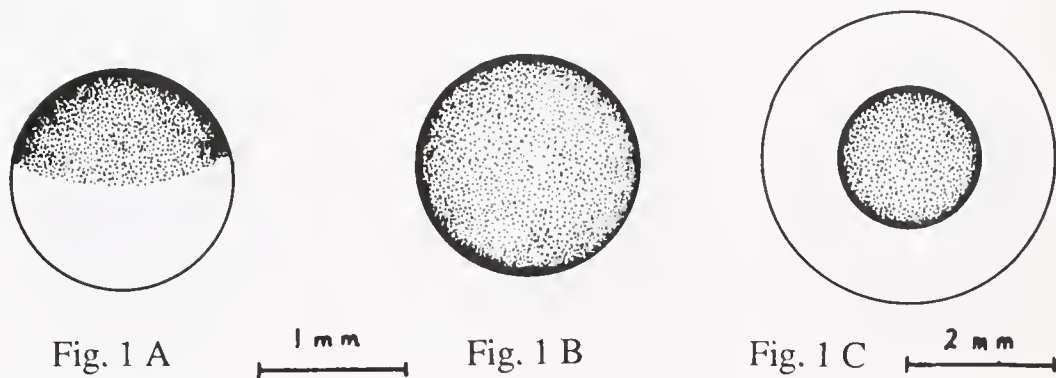


FIG. 1a, 1b, 1c, 1d, 1e, 2a, 2b, 3a, 3b. Embryonic development of *Rana rugulosa*. See text for details.



Fig. 4 A

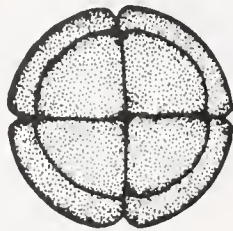


Fig. 4 B

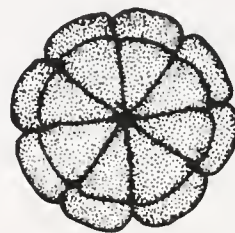


Fig. 5 A

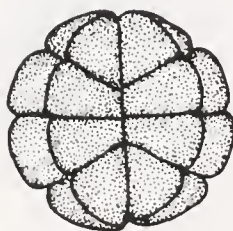


Fig. 5 B



Fig. 6 A

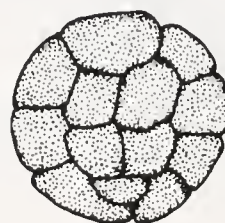


Fig. 6 B



Fig. 7 A



Fig. 7 B

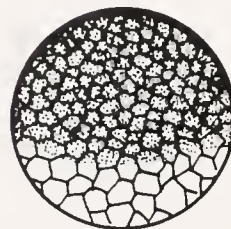


Fig. 8 A

FIG. 4a, 4b, 5a, 5b, 6a, 6b, 7a, 7b, 8a. Embryonic development of *Rana rugulosa*. See text for details.

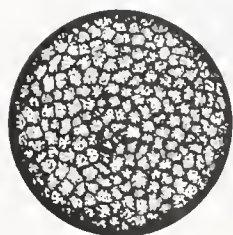


Fig. 8 B

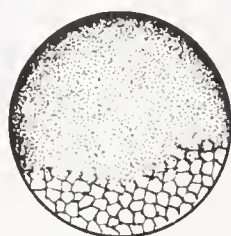


Fig. 9 A



Fig. 9 B



Fig. 10 A



Fig. 10 B



Fig. 11 A



Fig. 11 B



Fig. 12 A



Fig. 12 B

FIG. 8b, 9a, 9b, 10a, 10b, 11a, 11b, 12a, 12b. Embryonic development of *Rana rugulosa*. See text for details.



Fig. 12 C



Fig. 12 D

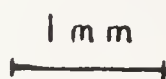


Fig. 13 A

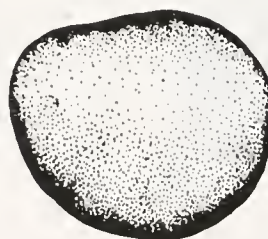


Fig. 13 B

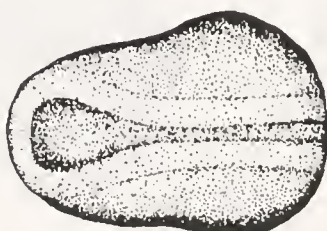


Fig. 14 A

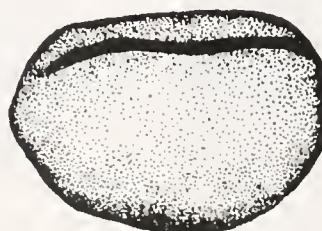


Fig. 14 B

FIG. 12c, 12d, 13a, 13b, 14a, 14b. Embryonic development of *Rana rugulosa*. See text for details.



Fig. 15 A

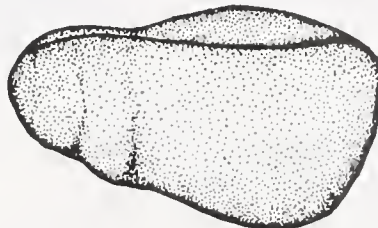


Fig. 15 B



Fig. 16 A

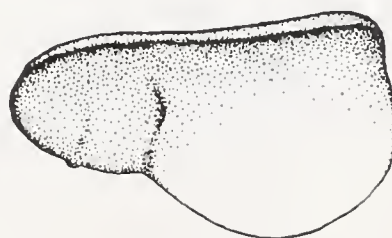


Fig. 16 B



Fig. 17 A



Fig. 17 B

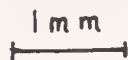


Fig. 17 C

FIG. 15a, 15b, 16a, 16b, 17a, 17b, 17c. Embryonic development of *Rana rugulosa*. See text for details.

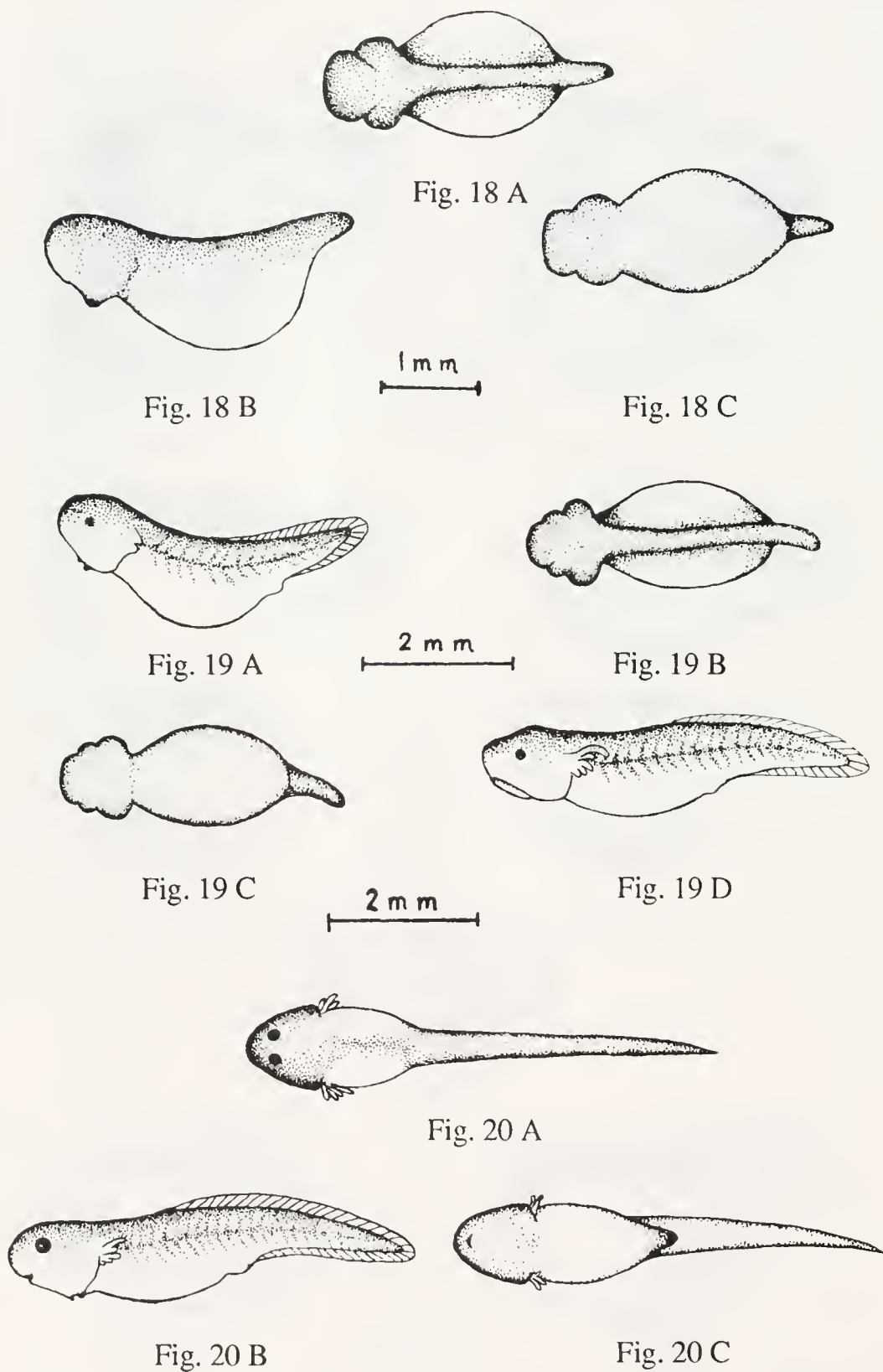


FIG. 18a, 18b, 18c, 19a, 19b, 19c, 19d, 20a, 20b, 20c. Embryonic development of *Rana rugulosa*. See text for details.



Fig. 21 A



Fig. 21 B



Fig. 21 C

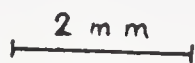


Fig. 22 A



Fig. 22 B



Fig. 22 C



Fig. 23 A



Fig. 23 B



Fig. 23 C

FIG. 21a, 21b, 21c, 22a, 22b, 22c, 23a, 23b, 23c. Embryonic development of *Rana rugulosa*. See text for details.



Fig. 24 A

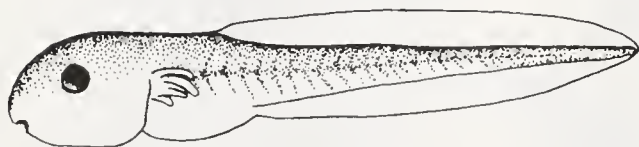


Fig. 24 B



Fig. 24 C

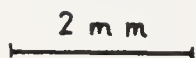


Fig. 25 A

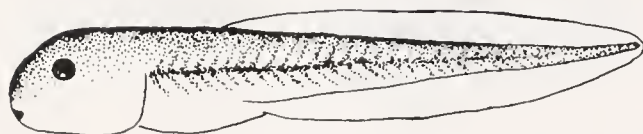


Fig. 25 B



Fig. 25 C

FIG. 24a, 24b, 24c, 25a, 25b, 25c. Embryonic development of *Rana rugulosa*. See text for details.



FIG. 26 (X30)



FIG. 27 (X30)



FIG. 28 (X30)



FIG. 29 (X30)



FIG. 30 (X30)



FIG. 31 (X30)

FIG. 26, 27, 28, 29, 30, 31. Embryonic development of *Rana rugulosa*. See text for details.



FIG. 32 (X30)



FIG. 33 (X30)



FIG. 34 (X30)



FIG. 35 (X30)



FIG. 36 (X30)



FIG. 37 (X30)

FIG. 32, 33, 34, 35, 36, 37. Embryonic development of *Rana rugulosa*. See text for details.



FIG. 38 (X30)



FIG. 39 (X30)



FIG. 40 (X30)



FIG. 41 (X30)



FIG. 42 (X30)



FIG. 43 (X20)

FIG.38, 39, 40, 41, 42, 43. Embryonic development of *Rana rugulosa*. See text for details.



FIG. 44 (X20)



FIG. 45 (X15)



FIG. 46 (X15)



FIG. 47 (X15)



FIG. 48 (X10)



FIG. 49 (X10)

FIG. 44, 45, 46, 47, 48, 49. Embryonic development of *Rana rugulosa*. See text for details.

The Validity of *Elaphe perlacea*, a Rare Endemic Snake from Sichuan Province, China

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Key Words: Reptilia, Serpentes, Colubridae, *Elaphe perlacea*, China, Sichuan, endemic, taxonomic validity.

Introduction

Recently Schulz (1989) reported on the validity of the specific status of *Elaphe perlacea* Stejneger, 1929. Schulz (1989) concluded, "Since data appear to be chiefly within the range of *E. mandarina*, *E. perlacea* is supposed to be placed in a subspecies rank of *E. mandarina* pointing out that further investigations may reveal that it is even a variety only." *Elaphe perlacea* is an endemic to Sichuan Province, China. For fifty years after the description of *Elaphe perlacea* by Stejneger (1929) no specimens were found. Many herpetologists including those of China doubted its validity.

In the last ten years three additional specimens have been found in Sichuan Province (Table 1, 2). Two of these specimens (80-1, 87-2, and 88-3) were examined by me. All three specimens have a dorsal scale formula of 19-19-17, 7 upper labials (the third and fourth entering the eye), one preocular, two post oculars, 1+2 temporals, and a divided anal. Both the scale counts and the patterns are similar to those of the type. The new material differs from that of the type in having: 1) Four

lower labials in contact with the anterior chin shield; 2) Dorsal scales of the male are smooth, only the posterior 2 to 3 middle rows are slightly keeled; 3) slight modification of the dorsal head pattern (Fig. 1).

Elaphe perlacea differs from *E. mandarina* (Cantor) in many ways. *E. mandarina* has: 1) 23 scale rows on the neck and mid-body, 19 or 21 before the vent; 2) Two anterior temporal scales (occasionally one); 3) A much different dorsal pattern. Thus, *Elaphe perlacea* is a valid species.

On a field trip during May of 1989 I went to Hailuo Gou one of the new localities. On the way we passed through a small town, Moxi. In the market were several *Elaphe perlacea* skins. This suggests that this snake is common in this area.

The type locality of *Elaphe perlacea* is Yachow Prefecture (Ya'an Prefecture), Sichuan Province, China. This is an imprecise locality since a prefecture is quite large. The two new localities are not in this prefecture but are close to it. The new

TABLE 1. *Elaphe perlacea* specimens found in Sichuan recently.

Sex, Number	Locality	Altitude (m)	Date	Snout-vent (mm)	Tail (mm)
Male	Hailuo Gou, Luding	2500	22 Oct 1987	—	—
Male, 87-2	Hailuo Gou, Luding	2500	22 Oct 1988	884	146
Female, 88-3	Hailuo Gou, Luding	2000	5 Jun 1988	1055	189
Female, 80-1	Wolong, Wenchuan	2000	Apr 1980	865	194

TABLE 2. Scale counts of *Elaphe perlacea* Stejneger, 1929.

Sex	Locality	Dorsal	Ventral	Anal	Subcaudal	Upper labial	Lower labial	Pre & post ocular	Temporal
M	Yachow, the type specimen	19-19-17	229	2	69/69+1	2-2-3	(3)	1-2	1+2
M	Hailuo Gou, Luding	19-19-17	231	2	62/62+1	2-2-3	9(4)	1-2	1+2
F	Wolong, Wenchuan	19-19-17	224	2	67/67+1	2-2-3	8/9(4)	1-2	1+2

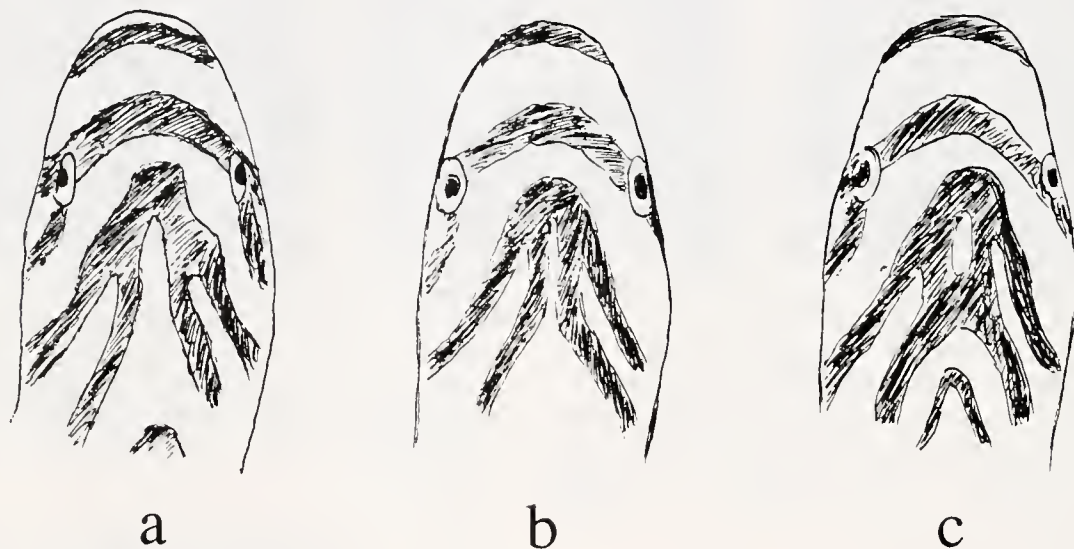
FIG. 1. Back of head of *Elaphe perlacea*, showing the main pattern. a. Male, type specimen. b. Female from Wolong. c. Male from Hailuo Gou.

FIG. 2. Map of Sichuan showing approximate position of localities.

localities are: Elev. 2000 and 2500 m, Hailuo Gou, Luding County, Garze Zang Autonomous Prefecture, and Elev. 2000 m, Wolong, Wenchuan County, Aba (Ngawa) Zang Autonomous Prefecture, Sichuan Province, China (Fig. 2). As presently understood *Elaphe perlacea* is endemic to Sichuan Province, China, and only occurs in the foot hills of the Himalayan Plateau directly west of the Sichuan Basin.

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Stellio sacra (Smith 1935) - a Distinct Species of Asiatic Rock Agamid from Tibet†

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Abstract. -An examination of the type series of *Agama himalayana sacra* Smith (1935) and new material collected in Tibet in 1988 has shown that this form should be considered a distinct species. In following the recent revision of the genus *Agama* (Moody 1980), *Stellio sacra* is included in the genus with all other Asiatic rock agamids.

Key Words: Reptilia, Sauria, Agamidae, *Stellio sacra*, Tibet, systematics, distribution.

Introduction

Four agamid lizards were collected at the beginning of the 20th Century near Lhasa, Tibet. They were described in a short account by Smith (1935) as a subspecies of the Himalayan rock agamid *Agama himalayana sacra*.

The examination of these type specimens and new material collected in Lhasa and the vicinity of Lhasa, Tibet in 1988 by the third and fourth authors, led us to the conclusion that it is not a subspecies of *Stellio himalayanus*. Furthermore it is not a member of the *Stellio himalayanus* species complex which includes *Stellio badakhshanus*, *Stellio chernovi*, *Stellio himalayanus*, and *Stellio stoliczkanus*. The results of the examination of the agamids from Lhasa, Tibet confirm the opinion of Ananjeva et al. (1981) that *Stellio sacra* should be elevated to full specific status.

According to the present revision of the genus *Agama* (Wermuth 1967) into *Agama*, *Stellio* (Moody 1980; Sokolovsky 1975, 1977) *Trapelus*, *Psuedotrapelus*, and *Xenagama* (Moody 1980) the lizards examined from Tibet should have the generic name, *Stellio*.

Methods

To the best of our knowledge all specimens housed outside the Peoples Republic of China were examined. Of the four specimens in the type series, one lectotype and two paralectotypes are housed at the British Museum (Natural History) [BMNH], and one paralectotype is housed at the Indian Museum, Calcutta (Zoological Survey of India [ZSI]). Thirteen additional specimens were collected during the 1988 joint Chengdu Institute of Biology - University of California Expedition and are housed at the California Academy of Sciences (CAS).

Stellio sacra (Smith 1935), new combination

Known Material

Material Examined:

Lectotype: BMNH 1946.8.28.57 (formerly 1904.12.28.1) [Fig. 1.]
Locality: Near Lhasa, Tibet.

Paralectotypes: BMNH 1946.8.28.58, BMNH 1946.8.28.59 [Fig. 2], and ZSI 15740 [Fig. 3]. Locality: near Lhasa, Tibet.

CAS 170545. Locality: Elev. 3740 m, Sera Monastery, Lhasa (29° 39' N 91°

† Sino-Soviet-American Arid Asian Desert Regions Research Paper no. 5.



FIG. 1. Lectotype of *Stellio sacra* BMNH 1946.8.28.57 (formerly 1904.12.28.1).

Sera Monastery, Lhasa (29° 39' N 91° 06' E), Lhasa Municipality, Xizang (Tibet) Autonomous Region, China. Collected by: T. J. Papenfuss and R. Macey. Date: 24 Sept., 1988.

CAS 170546-53. Locality: Elev. 3700 m, at base of mountains approx. 3 km WNW (airline) of the Potala Palace, Lhasa (29° 39' N 91° 06' E), Lhasa Municipality, Xizang (Tibet) Autonomous Region, China. Collected by: CAS 170546-49 R. Macey and T. J. Papenfuss, and CAS 170550-53 T. J. Papenfuss and R. Macey. Date: 25 Sept., 1988.

CAS 170554-57. Locality: Elev. 3990 m, 52.4 km south of Yangbajan (30° 13' N 90° 25' E), also at km 1900.8 from Xining, on the Xining-Golmud-Lhasa Rd., Lhasa Municipality, Xizang (Tibet) Autonomous Region, China. Collected by: CAS 170554-55 R. Macey and T. J.

Papenfuss, CAS 170556-57 T. J. Papenfuss and R. Macey. Date: 27 Sept., 1988. (See Table 1).

Other Material.

Note that the following material is reported on in Hu et al. (1987) but no numbers or reference to a museum collection are mentioned. It is probable that all or most of these specimens are housed at the Chengdu Institute of Biology.

Three males, 3 females, and 3 juveniles. Locality: Bomi (29° 50' N 95° 45' E), Qamdo Prefecture, Xizang (Tibet) Autonomous Region, China.

Six males, and 12 females. Locality: Lhasa (29° 39' N 91° 06' E), Lhasa Municipality, Xizang (Tibet) Autonomous Region, China.



FIG. 2. Paralectotypes of *Stellio sacra* BMNH 1946.8. 28.58 and BMNH 1946.8.28.59.

Two males, 2 females, and 1 juvenile. Locality: Nyningchi (29° 32' N 94° 25' E), Lhasa Municipality, Xizang (Tibet) Autonomous Region, China.

Distribution

Stellio sacra as presently understood, is restricted to the river drainage of the Yarlung Zangbo in the Lhasa Valley, Xizang (Tibet) Autonomous Region, China (Fig. 4). Only four localities are known, all between 3000 and 4000 m. Populations occurring in the Kunlun Mountains of southern Xinjiang Uygur Autonomous Region, China were previously assigned to *Stellio himalayanus himalayanus*, however their present taxonomic position is uncertain.

Diagnosis: Rock agamid with flattened head and body which is typical for this lizard group. They are comparatively large

lizards with a snout-vent length of 120-150 mm and a tail length of 180-240 mm (Table 1).

Gular Sac seems to be developed to a greater degree than in other *Stellio*. Body scales are small and granular. The scales are not well differentiated. There is a very slight but noticeable nuchal crest on the head. It begins from the middle of the occiput and continues as a poorly differentiated vertebral stripe. The longitudinal rows of enlarged and feebly keeled scales on the vertebral region are arranged parallel to each other. There are neither groups of enlarged scales nor separate enlarged scales on the dorsal lateral regions.

The males have a large patch of callous scales on the belly. The annuli and segmentation of the scales on the basal quarter of the tail are not prominent. On the



FIG. 3. Paralectotype of *Stellio sacra* ZSI 15740.

lateral surface of the tail there are three to four annuli in each segment.

There is a small granular dark pattern on the back. The center of the back tends to have more black and toward the sides a dark golden brown dominates. The separate elements of this pattern are connected to heavily marked diffuse transverse stripes. The narrow stripes form two rows of the dark colored scales that continue from the neck to the tail. Overall the lizard is darkly colored but there are a few randomly scattered yellow blotches on the back (Fig.5). Juveniles are lighter in color tending more toward a dark golden brown with darker speckling all over the

back. The dark golden brown forms bands across the back which are offset at the spine.

Comparative Description

Stellio sacra differs from *Stellio himalayanus* and related forms in all the diagnosis characters. *Stellio sacra* is only similar in body size to *Stellio stoliczkanus* among the species examined. Other species are notably smaller (Table 1; Anderson and Leviton 1969; Ananjeva et al. 1981).

The body proportion data concerning *Stellio sacra* and the *Stellio himalayanus* species complex indicates small differences

TABLE 1. Characters of *Stellio sacra* specimens used for analysis.

	Sex/age	Body length	Tail length	Hind limb length	Rostrum to front margin of tympanum	Number of scales at midbody
Type specimens						
BMNH 1946.8.28.57	M	136	215	98.5	30.5	232
BMNH 1946.8.28.58	F	130	autotomized	92.0	27.6	230
BMNH 1946.8.28.59	subadult	74	146	48.5	17.0	225
ZSI 15740	F	124	182	83.5	26.6	-
CAS specimens						
170555	M	147	246	92.2	33.6	249
170554	M	145	233	98.0	31.2	240
170556	M	143	autotomized	89.0	30.3	250
170546	F	114	188	74.0	24.3	230
170547	F	100	185	67.2	21.9	245
170548	F	100	autotomized	66.8	21.0	247
170545	juv.	67.0	128	45.0	14.8	225
170549	juv.	72.5	142	52.0	16.1	256
170550	juv.	71.0	137	48.0	15.7	246
170551	juv.	75.5	155	54.0	16.5	250
170552	juv.	75.0	136	52.0	16.2	234
170553	juv.	66.3	132	48.0	15.4	248
170557	juv.	82.5	146	61.0	18.0	223

(Table 2). *Stellio sacra* has a shorter tail than *Stellio badakhshanus*, *Stellio chernovi*, and *Stellio himalayanus*.

One of the paralectotypes, a female (BMNH 1946.8.28.58), has a regenerated tail. The length of the regenerated tail after autotomy is about 80 mm which is rather great. The scales of the tail are mucronate, and the regular annular arrangement in the regenerated portion of the tail is disturbed.

Stellio sacra has a more similar head height index to *Stellio erythrogaster* and *Stellio lehmanni* than to *Stellio caucasicus* and *Stellio himalayanus* (Ananjeva 1981); i.e. the head is not so flat (depressed).

It is necessary to also remark about the differences in the structure of the digits in *Stellio sacra* and that of the specimens examined of *Stellio caucasicus*, *Stellio lehmanni*, and *Stellio stoliczkanus* of the same size. The digits, and especially the terminal phalanges, of *Stellio sacra* specimens are not round in their section as in the above group of species, but instead are compressed laterally.

The distinctive character of *Stellio sacra* pholidosis is its comparative homogeneity. The scales on the back, sides and belly are small. It has a considerably large scale count around the mid-body of 239 scales. The mid-body scale count of *Stellio badakhshanus*, *Stellio chernovi*, *Stellio himalayanus*, and *Stellio stoliczkanus* all do not exceed 180 scales. Such a large mid-body scale count is only observed in *Stellio nuristanicus*, which has from 230-248 mid-body scales. During this phase of our study two of the type specimens (Anderson and Leviton 1969) were examined.

The longitudinal rows of the enlarged poorly keeled scales are not arranged as the obvious "dorsal stripe," as typically observed in many other species of *Stellio*. The dorsal scales gradually decrease in size and degree of keeling, from the center of the back toward the small dorso-ventral scales. The ventral scales are smaller than the dorsal scales. The posterior margins of these scales slightly overlap the scales of the following row.



FIG. 4. Distribution of *Stellio himalayanus* and *Stellio sacra*. Question mark indicates Xinjiang Autonomous Region population of questionable taxonomic status.

The ventral head scales are also small and not regular. The size of these scales decreases from the nasal end toward the gular fold. On the sides of the head and on the neck are situated small groups of very strongly keeled spinose scales.

Stellio sacra has nostrils shaped longitudinally oval, similar to *Stellio chernovi* and *Stellio himalayanus*. Where as *Stellio agorensis*, *Stellio melanurus*, *Stellio nuristanicus* and *Stellio tuberculatus* have round nostrils. *Stellio sacra* has a round tympanum.

In *Stellio sacra*, the scales of the upper surface of the fore and hind limbs are comparatively small, but their size is similar to the largest dorsal scales. These scales are strongly keeled. Single slightly enlarged scales are distinguishable from the

surrounding small scales. The scales on the base of the tail are keeled and mucronate, but to a smaller degree than for example in *Stellio himalayanus*.

The results of the comparative study of Asiatic rock agamids enables the typical distinguishing characters of *Stellio sacra* to be identified:

1. The small size of the scales.

2. The presence of a short nuchal crest made up of from two to three scale rows of slightly enlarged, narrow, keeled, dark colored scales. Such a nuchal crest is absent in *Stellio chernovi*, *Stellio himalayanus*, *Stellio stoliczkanus* and other species. A nuchal crest is noted however in *Stellio melanurus*, *Stellio nuptus*, *Stellio Stellio*, and *Stellio tuberculatus*.



FIG. 5. *Stellio sacra* from elevation 3990 m, 52.4 km south of Yangbajan (30° 13' N 90° 25' E), Xizang (Tibet) Autonomous Region, China.

3. The ends of the occipital (nuchal) and neck scales are directed backwards but not foreword; the parietal scales are oriented in a laterocaudal direction.

4. The rows of the enlarged dorsal scales are parallel but do not meet as in species of the "*Stellio himalayanus* " complex.

TABLE 2. Comparative data on the relative proportions of the tail, limbs, and head of rock agamids of the genus *Stellio* (*S. sacra* and agamids of the *S. himalayanus* complex).

Species	n		tail length/ body length		hind limb length/ body length (%)		head length/ body length (%)	
	Male	Female	Male	Female	Male	Female	Male	Female
<i>Stellio sacra</i>	5	4	1.61	1.58	72.2	69.0	27.0	25.1
<i>Stellio stoliczkanus</i>	35	14	1.65	1.48	66.3	63.7	25.9	25.1
<i>Stellio himalayanus</i>	11	15	1.88	1.75	67.9	66.7	26.3	25.7
<i>Stellio badakhshanus</i>	3	1	1.72	1.67	76.0	70.0	27.3	26.2
<i>Stellio chernovi</i>	18	8	1.85	1.77	77.2	74.0	27.6	26.3



FIG. 6. Habitat of *Stellio sacra*, elevation 3990 m, 52.4 km south of Yangbajan (30° 13' N 90° 25' E), Xizang (Tibet) Autonomous Region, China.

5. In the region over the shoulders there are two arched diffuse rows of slightly enlarged mucronate (spinose) scales.

6. The absence of enlarged scales or regions of enlarged scales on the back of the body.

7. The upper head scales distributed between the nasal scales have a stretched shape. The length of these scales is twice the width as also in *Stellio agorensis*, *Stellio nuristanicus*, and *Stellio tuberculatus* where as the scales of *Stellio chernovi* and *Stellio himalayanus* have a roundish, polygonal shape.

8. Only a single row of small scales is noted between the suboculars and the supralabials. Other species have two to

five scale rows.

9. The scales of the back, shoulders, thighs and some parietal scales have an unusual microstructure. The margins of the scales are jagged resembling that of fringes. This character was also observed in *Stellio annectens*, *Stellio erythrogaster*, *Stellio melanurus*, and *Stellio nuptus*.

10. There is a patch of callous (granular) scales in the middle of the belly, which is large in males.

11. The males have a large patch of anal pores and from six to seven rows of callous scales before the cloaca.

Coloration

The dorsal coloration of the type

specimens consists of diffuse components, each scale is either totally dark or light in coloration. The parietal region and along the middle of the back (two scale rows of absolutely dark scales) are more dark in coloration. From the middle of the back to the sides there are light brown transverse stripes. This coloration is poorly developed in some specimens.

The subadult specimen has a similar small speckled pattern and in addition has alternating light and dark transverse stripes coming from the vertebral ridge toward the sides of the body. This pattern is similar to that of juvenile specimens of *Stellio tuberculatus*.

As far as we can tell from the available specimens of *Stellio sacra*, no contrasting pattern and coloration on the surface of the gular region, neck and nuchal region are noted. Such a contrasting pattern and coloration are typical for specimens of *Stellio himalayanus* and related species.

Natural History

Stellio sacra are common in the rocky hills surrounding the Lhasa Valley. They were seen only on slopes covered with large boulders (Fig. 6). Often a single adult male occupied a pile of boulders in association with several females and juveniles. *Stellio sacra* is an agile, alert species that is difficult to approach closely. The only other reptile that occurs on the rocky slopes is the gecko, *Cyrtodactylus tibetanus*. Another agamid, *Phrynocephalus theobaldi* is abundant on the sandy soil at the base of the rocky hills.

Discussion

The large review of the rich Indian fauna that Smith (1935) dealt with explains why the Sacred Agamid, *Stellio sacra*, was originally described as a subspecies of the Himalayan agamid, *Stellio himalayanus*. The study presented here concludes that *Stellio sacra* is not related to the *Stellio himalayanus* complex. On the other hand the above descriptions of the morphological characters do not allow an interpretation of the direct relation of *Stellio sacra* to such

species as *Stellio agrorensis*, *Stellio melanurus*, *Stellio nuptus*, and *Stellio tuberculatus*. The characters which enable us to bring together *Stellio sacra* and these species should be considered as plesiomorphic similarities. These characters are long limbs, the presence of a small gular sac and nuchal crest, the polyannular structure of the caudal segments, the juvenile color pattern, and so on. This assumption about a plesiomorphic condition is based on the idea that the oligomerization (decreasing of number of elements) of homologous organs (here pholidosis elements) is one of the main directions of agamid evolution (Dogel 1954).

Characters, such as the orientation of the scale axes in nuchal and neck regions and in parietal scales is also of great interest. It is suggested (Peters unpublished data) that the more common condition of the scale, i.e. the orientation of the point backwards, is typical not only for most of the species in the genus *Stellio* (including *Stellio sacra*), but also for the majority of agamids and lizards as a whole. Hence it is a plesiomorphic condition. The contrary direction, where the point of the scale is forwards, is observed in *Stellio melanurus*, *Stellio nuptus* and a number of African species. In accordance with Peter's point of view, this should be considered as an apomorphic condition. However there is a problem in interpreting such a character as the presence of the scales with the jagged margins. This scale structure is found in species with both types of scale orientation, including *Stellio sacra* as well as *Stellio erythrogaster*, *Stellio melanurus*, *Stellio nuptus* and the African species, *Stellio annectens*. The interpretation of such characters makes all possible explanations of the relationships of these species controversial.

These facts and the inability at this time to determine even a single obvious synapomorphy for all Asiatic rock agamids of the genus *Stellio* (with or without *Stellio melanurus* and *Stellio nuptus*) does not allow an acceptable phylogenetic relationship to be developed. This problem

TABLE 3. The distribution of the species in the genus *Stellio*.

Species	Distribution
<i>Stellio adramitana</i> (Anderson 1896)	Arabia
<i>Stellio agrorensis</i> (Stoliczka 1872)	Afghanistan, Pakistan, India
<i>Stellio annectens</i> (Blanford 1870)	Africa (Somalia, Ethiopia)
<i>Stellio atricollis</i> (Smith 1849)	Eastern and southern Africa
<i>Stellio badakhshanus</i> (Anderson and Leviton 1969)	Afghanistan
<i>Stellio caucasi</i> (Eichwald 1831)	Caucasus, Tadjikistan, Turkmania, Turkey, Iraq, Iran, Afghanistan, Pakistan
<i>Stellio chernovi</i> (Ananjeva, Peters, and Rzepakovsky 1981)	Tadjikistan, Turkmania, Uzbekistan
<i>Stellio cyanogaster</i> (Ruppell 1835)	Somalia, Ethiopia
<i>Stellio erythrogaster</i> (Nikolsky 1896)	Iran, Turkmania
<i>Stellio himalayanus</i> (Steindachner 1869)	Tadjikistan, Uzbekistan, Afghanistan, Pakistan, India
<i>Stellio lehmanni</i> (Nikolsky 1896)	Tadjikistan, Turkmania, Uzbekistan, Afghanistan
<i>Stellio melanurus</i> (Blyth 1854)	Iran, Pakistan
<i>Stellio microlepis</i> (Blanford 1874)	Iran
<i>Stellio nuptus</i> (De Filippi 1843)	Iraq, Iran, Afghanistan, Pakistan
<i>Stellio nuristanicus</i> (Anderson and Leviton 1969)	Afghanistan
<i>Stellio phillipsii</i> (Boulenger 1895)	Ethiopia
<i>Stellio sacra</i> (Smith 1935)	Tibet
<i>Stellio stellio</i> (Linnaeus 1758)	Greece, southwest Asia, northern Egypt
<i>Stellio stoliczkanus</i> (Blanford 1875)	Mongolia, China
<i>Stellio trachypleurus</i> (Peters 1982)	Ethiopia
<i>Stellio tuberculatus</i> (Hardwicke and Gray 1827)	India, Nepal, Afghanistan, Pakistan
<i>Stellio yemenensis</i> (Klauzewitz 1954)	Arabia
<i>Stellio zonorus</i> (Boulenger 1895)	Somalia

may be explained not only by the small sample size of *Stellio sacra* and the fact that many other forms are poorly studied but also by the obvious existence of parallel trends in different developmental lines within this lizard group.

In order to arrive at a more trust worthy hypothesis of the relationships of rock agamids, it is necessary to carry out biochemical investigations. The first preliminary results of such investigations are that of Joger and Arano (1987) and Ananjeva and Sokolova (in prep.). This type of data will be highly interesting to compare with the results of comparative morphological studies.

The distributional patterns of Asiatic rock agamids of the genus *Stellio* (Table 3) and their chorological isolation seems to support the idea that *Stellio* is a

monophyletic group. Rock agamids of the genus *Stellio* are distributed from Greece and the Nile River Delta in the west to the Gobi Altai of southern Mongolia, and the western deserts of China in the east. In the western part of this region, Greece to the Nile River Delta, *Stellio stellio* is found. The southern portion of this region from southwestern Iran to Pakistan *Stellio melanurus* and *Stellio nuptus* occur. These species are probably of African origin (Peters unpublished). In southern Iran and Afghanistan along with *Stellio melanurus* and *Stellio nuptus* also occur *Stellio agrorensis*, *Stellio badakhshanus*, *Stellio caucasi*, *Stellio erythrogaster*, *Stellio himalayanus*, *Stellio microlepis*, and *Stellio nuristanicus*.

The Asiatic rock agamids of the genus *Stellio sensu stricto* are absent from the mountainous regions of western Indostan

and the eastern portion of the Arabian Peninsula. They are also not found across the Red Sea in Ethiopia and Somalia. These areas are poorly studied herpetologically and it is possible that they do in fact occur in these regions.

The distribution of Asiatic rock agamids seems to be a single unit. Most problematic is the origin of such species as *Stellio melanurus*, *Stellio nuptus*, and *Stellio stellio*, which may be of African origin as it was already mentioned above.

It is possible that this assumption will be corroborated during further research in biochemical phylogeny. The preliminary results of Joger and Arano (1987) on *Stellio stellio* is a first step. The origin of the genus *Stellio* is interesting and the data about the early divergence of *Stellio* in *Stellio sensu stricto* (Asiatic species) and the *Stellio atricollis* species group from Africa and southern Arabia is useful (Joger and Arano 1987). It is possible that *Stellio* is a paraphyletic group of species. The Arabian - African species group is *Stellio adramitana*, *Stellio annectens*, *Stellio atricollis*, *Stellio cyanogaster*, *Stellio phillipsi*, *Stellio trachypleurus*, *Stellio yemenensis*, and *Stellio zonurus* (Table 3). These species are similar to the Asiatic species *Stellio melanurus* and *Stellio nuptus* in a number of characters. This allows an assumption that they are related.

Acknowledgments

We are most grateful for the loan of type material of *Stellio sacra* from Dr. A. C. G. Grandison, Dr. E. H. Arnold and Dr. A. F. Stimson of the British Museum of Natural History, London, Great Britain, and Dr. Shara of the Indian Museum, Calcutta, India.

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Isolation and Amino Acid Sequence of a New Dodecapeptide from the Skin of *Oreolalax pingii* †

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Abstract. -A novel dodecapeptide has been isolated by alumina column chromatography and HPLC from methanol extracts of the skin of the Chinese frog *Oreolalax pingii*. The sequence of the peptide is: Gly-Leu-Val-Ser-Asp-Leu-Met-Tyr-Gly-Ile-Gly-Leu-NH₂. This peptide differs from all the other amphibian skin peptides and should be regarded as a member of a new peptide family.

Key Words: Amphibia, Anura, Pelobatidae, *Oreolalax pingii*, China, biochemistry, peptides.

Introduction

Many active peptides have been discovered from amphibian skin during the past 20 years or more. Amphibian skin peptides have proved to be of considerable value not only in pharmacology, but also in taxonomic and evolutionary domains (Erspamer 1984; Cei 1985; Lazarus et al. 1985). In order to discover new active peptides, we have carried out research on amphibian skin peptides from Chinese frogs since 1983 (Hua et al. 1985; Tang et al. 1985). This paper concerns another novel dodecapeptide obtained from the skin of *Oreolalax pingii*.

Methods

The materials and experimental procedures were previously reported (Tang et al. 1985), with the following brief mentions and additions.

Six hundred specimens of *Oreolalax pingii* were collected in May, 1983 from the Daliangshan of Sichuan Province, China. The fresh skins (400 g) were removed and extracted with methanol. The methanol extracts were evaporated until dry. The residue was dissolved in 95% ethanol and the solution distributed on the alumina

columns. The column was eluted with ethanol-water mixtures of descending concentrations of ethanol (also see Montecucchi et al. 1981)

HPLC was performed on a Waters HPLC system. Details of individual chromatographic procedure are shown in the figures. Amino acid analysis of peptides after hydrolysis in HCl were carried out on a LKB 4400 amino acid analyzer. Sequence analysis of the peptides were performed by manual DABITC/PITC procedure (Chang 1983). The complete sequence analysis of the dodecapeptide was carried out on an Applied Biosystems Model 470A gas phase sequencer.

Enzymatic digestions of the peptide with α -Chymotrypsin, carboxypeptidase A (CP-A) and Y (CP-Y) were also as before (Tang et al. 1985). Bioassays of each isolated product were tested on the longitudinal muscle myenteric plexus preparation of the guinea pig ileum (GPI),

Results

The water portion eluted from alumina columns was lyophilized to give 214 mg of residue. The residue was separated by HPLC semi-preparatively as in Fig. 1. Perks 32 and 33 each were single peak by verifying on HPLC (analytical μ Bondapak C₁₈ column, the elution conditions were the same as in Fig. 1), respectively. The

† This publication combines material previously published in Chinese by Tang et al (1985) with additional information.

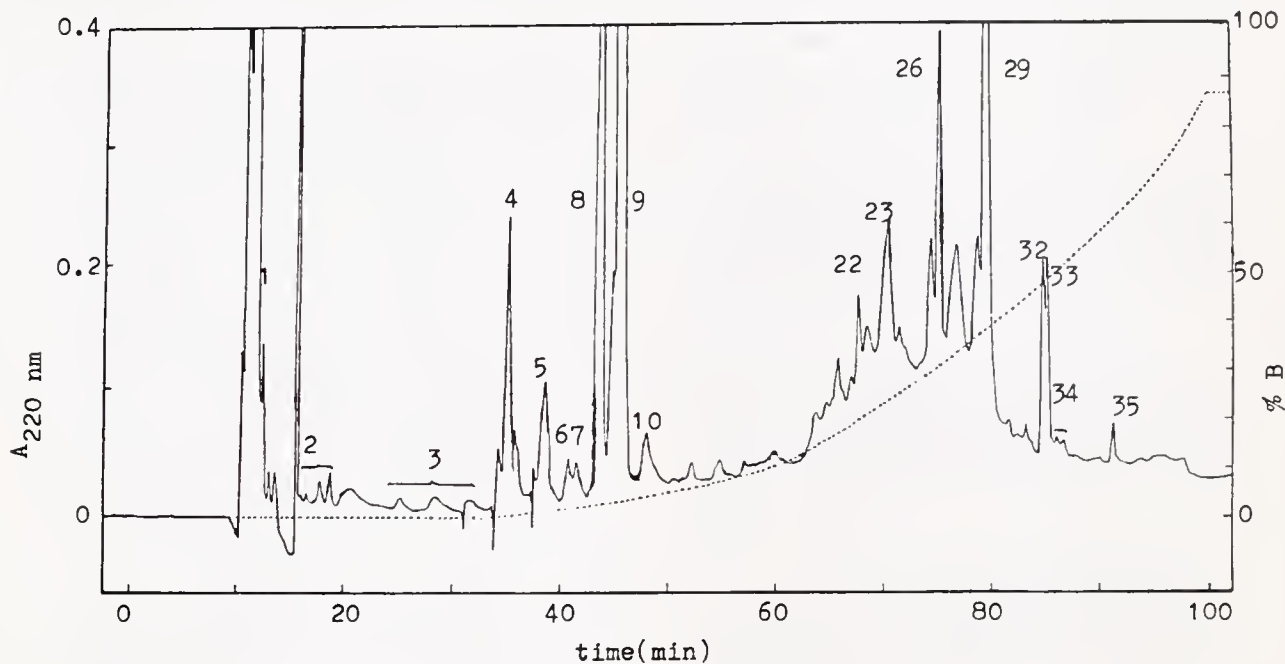


FIG. 1. RP-HPLC of the water eluate from the alumina columns. Column: μ Bondapak C_{18} 7.8X300 mm. Mobile phase: A=0.05% CF_3COOH B=60% CH_3CN in A. Concave gradient elution from 0–85%B (dotted line), 90 min, at 1.0 ml/min. Detected at UV 220 nm, 0.4 aufs.

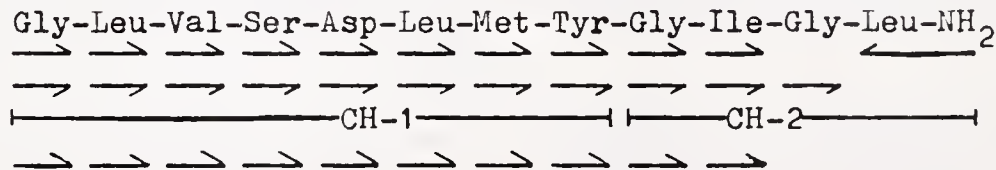


FIG. 2. Profile of sequence analysis of the dodecapeptide. ($\rightarrow$): DABITC/PITC method. ($\rightarrow$): gas phase sequencing. ($\leftarrow$): CP-Y digestion. CH: α -chymotryptic peptides.

difference of retention time of the two peaks was 0.8 min. The peak 32 acted as the representative of the dodecapeptide for further studies and the peak 33 was also investigated simultaneously.

Amino acid composition of the peak 32 was Asp (1), Ser (1), Gly (3), Val (1), Met (1), Ile (1), Leu (3), Tyr (1). Amino acid sequence of the peak 32 was determined by the DABITC/PITC method and gas phase sequencing. The former method proceeded to the tenth step, but the latter to the penultimate residue (Fig. 2). For C-terminal residue analysis, CP-A and CP-Y digestions of the peak 32 were carried out,

and did not release any amino acids by the former. This indicated a blocked C-terminus; upon latter, however, Leu and Gly were obtained. Thus, we deduced that the C-terminal structure of the peak 32 is $Leu-NH_2$. Digestion of the peptide by α -chymotrypsin provided further structural confirmation. The fragment peptides, CH-1 and CH-2 were separated on HPLC as depicted in Fig. 3. Amino acid compositions of the two fragments are in accordance with their sequences (see Fig. 2), respectively.

From the above results the complete amino acid sequence of the peak 32 was

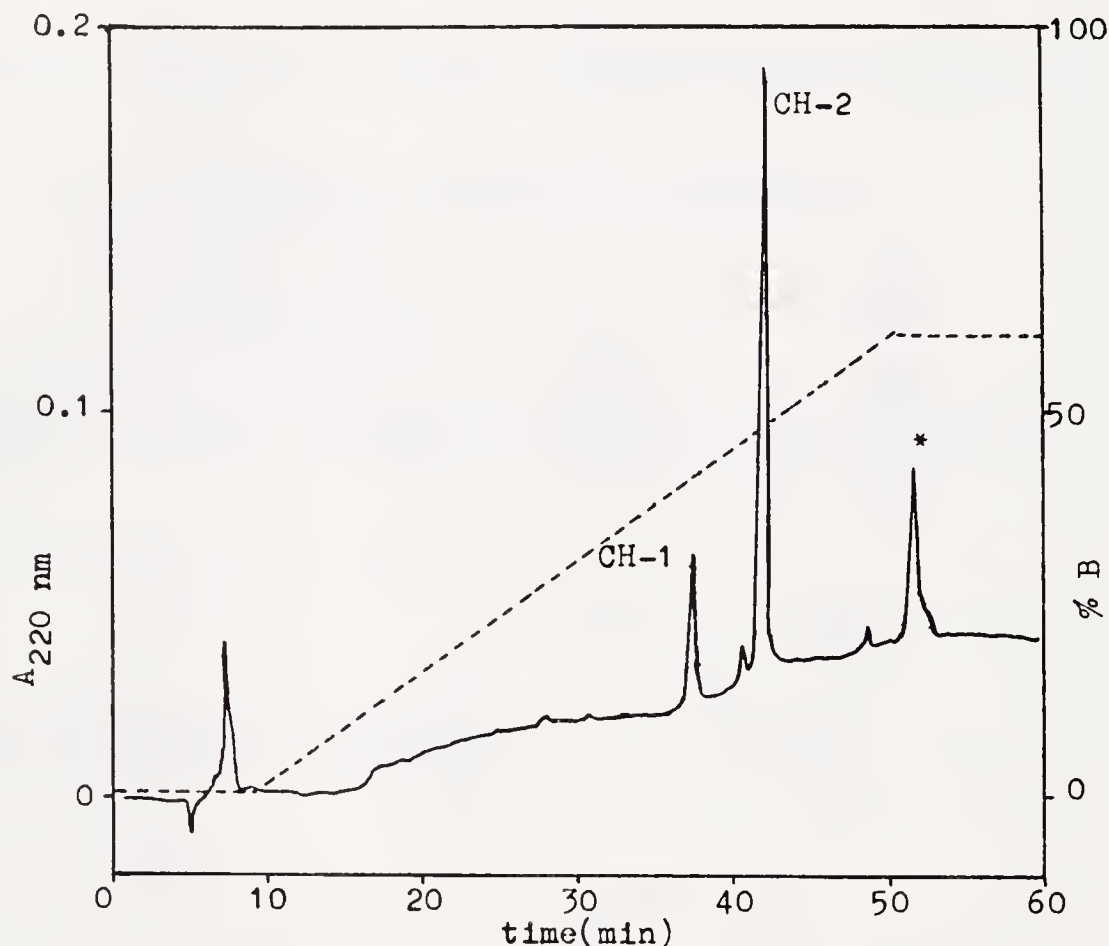


FIG. 3. RP-HPLC of α -chymotryptic digests of the dodecapeptide. Column: μ Bondapak C_{18} 3.9X300 mm. Mobile phase: A=0.1% CF_3COOH B=60% CH_3CN in A. Linear gradient elution from 0–60%B, 40 min, at 0.6 ml/min. Detected at UV 220 nm, 0.2 aufs. Peak (*) is the unreacted dodecapeptide.

established as in Fig. 2.

The peak 33 had the same properties with the peak 32 in the amino acid compositions and sequence analysis, respectively. We do not know the structural differences between the two peaks.

Based on the amino acid analysis, the yield of the pure dodecapeptide (including peak 32 and 33 in Fig. 1) was estimated to be at least 1.0 nmol starting from 1.0 g of fresh skin, according to that the rate of recovery of all above isolation steps was 10%. The dodecapeptide was inactive in GPI test, and its activity awaits to be established by assay methods other than those used in the present screening.

Discussion

The dodecapeptide described above is a completely novel peptide. The peptide may be a member of a new peptide family, and it should be regarded as the biochemical characteristic of *Oreolalax pingii* in taxonomy. Furthermore, the C-terminal portion of the dodecapeptide has some homologies to the mammalian Leu-enkephalin (Hughes et al. 1975) as shown below:

The dodecapeptide: Gly-Leu-Val-Ser-Asp-Leu-Met-Try-Gly-Ile-Gly-Leu-NH₂

Leu-enkephalin: Try-Gly-Gly-Phe-Leu

In amphibian skin peptide research, it

was observed that one peptide can be separated by HPLC into two components--the peak splitting, such as that discovered in HPLC separation of PGL-a (Andreu et al. 1985) and ranamargatin (Tang et al. 1988). The peak 32 and 33 (Fig. 1) both have the same amino acid composition and sequence. Therefore, they may be produced by one peptide in HPLC separation. The reason of the peak splitting mentioned above, however, is presently not known. To our knowledge, there are no similar findings besides the amphibian skin peptides. Hence, it is necessary to understand if the peak splitting is unique to the amphibian skin peptides.

Acknowledgments

We thank Mr. C. Chen for amino acid analysis.

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The Validity of *Sacalia quadriocellata*

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Key Words: Reptilia, Testudines, Emydidae, *Sacalia quadriocellata*, China, taxonomic validity.

Introduction

Sacalia quadriocellata was first described by Siebenzock in 1903 as *Clemmys bealei quadriocellata*. Pope (1935) described *Clemmys quadriocellata* from Hainan, and compared it with *Clemmys bealei*. But most people except Pope thought that *S. quadriocellata* was a synonym of *S. bealei*. Sachsse (1984a) held that it was the female of *S. bealei*.

Methods

Specimens of *Sacalia quadriocellata* from Hainan and Guangxi provinces, along with specimens of *S. bealei* from Hainan, Fujian and Anhui provinces were examined. Data were taken on external, skull, and shell suture characters. Sexual differences were also examined.

Results

External differences

1) The dorsal surface of the head is uniform olive or chocolate brown in *Sacalia quadriocellata*, but it is vermiculated with black in *S. bealei*.

2) *Sacalia quadriocellata* have two ocelli on each side of the dorsal surface of the head. The ocelli always have distinct boundaries and there is one black spot within each ocellus (Fig. 1). In contrast, *S. bealei* have one or two ocelli on each side of the dorsal surface of the head (Fig. 1). If two ocelli are present, they may not have clear boundaries, but tend to run together. There are from one to three black spots within each ocellus.

3) The anterior margin of the carapace has many little black or chocolate brown speckles in *Sacalia bealei*. There are few or none in *S. quadriocellata*.

Differences in skull characters

1) The length from anterior of prefrontal to posterior of basi occipital to supra occipital is 2.59-2.62 (N = 3) in *S. bealei*; but 2.92-3.39 (N = 3) in *S. quadriocellata*.

2) The quadrate is not in contact with the opisthotic in *Sacalia bealei*, but in *S. quadriocellata* the posterior part of the quadrate tends to contact the opisthotic.

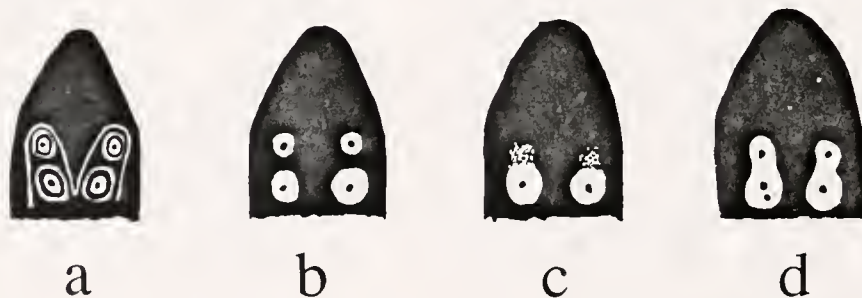


FIG. 1. Ocelli of *Sacalia quadriocellata* and *S. bealei*. A: Male *S. quadriocellata*. B: Female *S. quadriocellata*. C: *S. bealei* with a pair of ocelli. D: *S. bealei* with two pairs of ocelli.

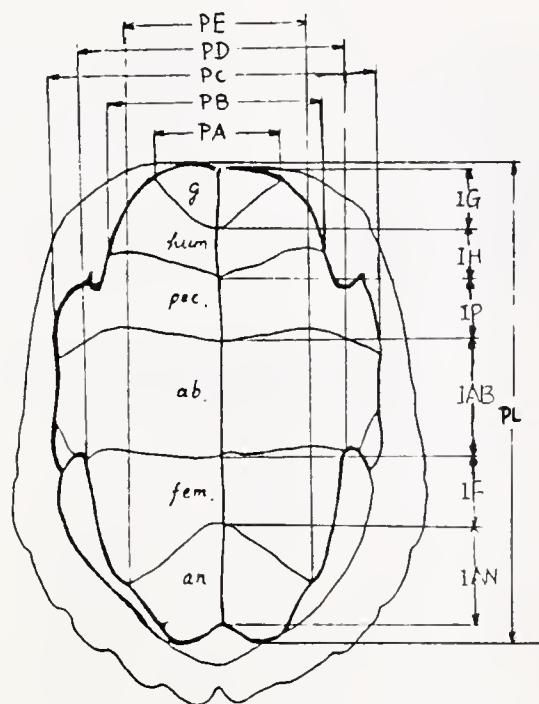


FIG. 2. Means of measurement of shell sutures.

TABLE 1. Analysis of shell suture data. See Fig. 2 for details of measurement.

Measure	<i>Sacalia bealei</i> (N=27)	<i>Sacalia quadriocellata</i> (N=26)
	mean $\pm$ SE	mean $\pm$ SE
PA/PL	0.259 $\pm$ 0.0180	0.249 $\pm$ 0.0137
PB/PL	0.424 $\pm$ 0.0240	0.417 $\pm$ 0.0207
PC/PL	0.620 $\pm$ 0.0280	0.616 $\pm$ 0.0337
PD/PL	0.501 $\pm$ 0.0198	0.520 $\pm$ 0.0226
PE/PL	0.377 $\pm$ 0.0140	0.367 $\pm$ 0.0140
IG/PL	0.114 $\pm$ 0.0140	0.109 $\pm$ 0.0117
IH/PL	0.105 $\pm$ 0.0160	0.096 $\pm$ 0.0150
IP/PL	0.171 $\pm$ 0.0240	0.169 $\pm$ 0.0172
IAB/PL	0.230 $\pm$ 0.0177	0.248 $\pm$ 0.0218
IF/PL	0.164 $\pm$ 0.0140	0.157 $\pm$ 0.0154
IAN/PL	0.194 $\pm$ 0.0163	0.180 $\pm$ 0.0168
BL/PL	0.359 $\pm$ 0.0200	0.370 $\pm$ 0.0163
FL/PL	0.387 $\pm$ 0.050	0.383 $\pm$ 0.0150

3) The posterior process of the jugal turns up in *S. bealei*, but turns down in *S. quadriocellata*.

4) The shortest distance between the orbital is located at the anterior prefrontal in *Sacalia bealei*. It is located at the joint of the frontal and prefrontal in *S. quadriocellata*.

Shell suture differences

Thirteen shell suture characters in *S. bealei* (N = 27) and *S. quadriocellata* (N = 26) were analyzed (Fig. 2). Seven characters (PA/PL, PB/PL, PE/PL, IH/PL, IAB/PL, IAN/PL, BL/PL) are different from each other (t, $p < 0.05$), [Table 1].

Sexual dimorphism

Sexual dimorphism was evident in *Sacalia quadriocellata*. In life, males have very distinct orange-red speckles near the neck and limbs, whereas females have not.

The carapace is narrower at the anterior end than the posterior end in females, but both

ends are nearly equal in males. The most interesting character is ocelli coloration. They tend to be greyish with a white ring surrounding the two ocelli on each side in males (Fig. 1), but tend to be yellow without a white ring in females. The skulls of the males were somewhat flat, narrow and long. The skulls of the females were somewhat convex, wide and short.

Discussion

Since *Sacalia bealei* and *S. quadriocellata* have distinguishable characters, we consider *S. quadriocellata* to be a valid name. *Sacalia quadriocellata* occurs in China on Hainan Island and Guangxi Province. It is also found in central Annam. The specimens reported on by Zheng and Ding (1965) from Fujian Province and by Zhong (1981) from Jiangxi Province are misidentified *S. bealei*. The later species ranges over most of southern China, including Guizhou, Anhui, Jiangxi, Fujian, Guangdong provinces, Hainan Island, and Hong Kong.

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Interim Report on the Freshwater Turtle Trade in Bangladesh

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Key Words: Reptilia, Testudines, Bangladesh, conservation, commercial trade.

Introduction

Trade in the freshwater turtle species of Bangladesh has been occurring for a very long time. Exploitation of this natural resource was limited prior to 1980, but during the past decade there has been a rapid and drastic increase both in terms of commercial exploitation and volume of trade. At present freshwater turtles are captured everywhere in the country. Since there are potential buyers, who have emerged due to the increase in turtle trade, the hunters prefer to sell their catches to those buyers rather than selling it in the small country markets.

Turtle meat has served as a source of protein to most of the ethnic groups and non-moslems in Bangladesh. The turtle meat and eggs are mostly consumed by the Hindus and to some extent by the Christians, Buddhists and other minorities. Recent observations indicate that the rate of turtle meat consumption has accelerated due to the high price of other meat sources, making them unaffordable to most people, as well as the scarcity of fish and meat products. This trend has already proved to be a threat to the chelonian population. Many of the freshwater turtles are becoming rarer. Personal observations and interviews with the local people and hunters (turtle catchers) have confirmed it.

Lack of turtle trade regulation is also one of the reasons for the increase in the magnitude of turtle trade. Though on paper the Forest Department, "godfather" of all the wildlife in Bangladesh, looks after it practically there is no one to execute the regulation. There is no regulation to control the hunting and capturing of the

turtles. As a result, freshwater turtles are exported all round the year though the bulk fluctuates with the season. Some of the freshwater turtles are included in CITES I, but trade is still continuing. The Bangladesh Wildlife (Preservation Amendment) Act, 1973 does not include any turtle species in its schedules and as such gives free access to the exporters. Moreover the government also charges a nominal amount of duty (Taka 5.00 per maund) on the export.

Study Period

This is a preliminary report on the freshwater turtle trade in Bangladesh, covering the period from May 1989 to mid-August, 1989. The work is still in progress and the final report will be submitted after the completion of the study.

Objectives

The primary objectives of this study are to identify/determine:

1. Species involved in trade.
2. Volume of trade.
3. Proportion of each species exported.
4. Methods of collecting.
5. Major collecting sites, habitat preferences of the species concerned.
6. Sex ratio of the species exported.
7. Status of the species in the wild involved in trade.
8. Methods of transportation, packing, stocking.
9. Mortality rate during transportation.

Previous Information

The chelonian fauna of Bangladesh are

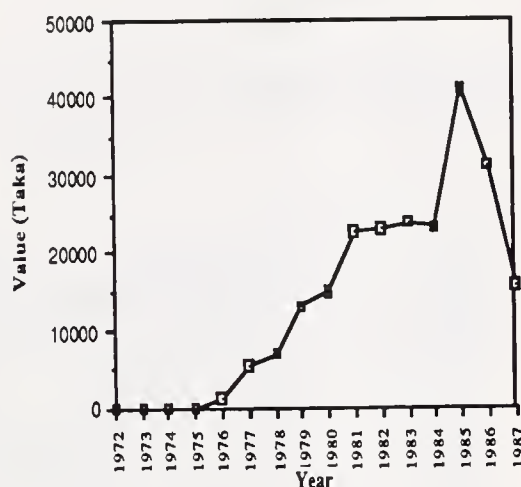


FIG. 1. Monetary value in Bangladesh Taka of turtle export from 1972 through 1987. The current exchange rate is approximately \$1 US = Taka 30. Figures are as reported by the Bangladesh Export Promotion Bureau.

not well documented. We have to rely mostly on Smith (1931), and it is necessary to revise and update the information for most of the chelonians. Later works include that of Ahmed (1958), Shafi and Quddus (1977), Husain (1979), Khan (1982, 1985) and Fugler (1984). All these publications throw some light on the chelonians with some indication of the species being exploited for trade either locally or for export. Fugler (1984) put forward further information on the extent of trade and the species involved. But since he worked for a very short time much information is lacking. A recent study by Hosain (1989 unpublished) gives some information on the food and feeding habits of some freshwater turtles in Bangladesh. Information on turtle export is also on file at the Export Promotion Bureau (EPB). They only give the value of the turtles exported (Fig. 1). Neither the quantity nor the species are known.

Methods

Based on earlier information regarding the location of some of the turtle export

centers, those centers were visited and the owners were briefed about our intention to collect information on the turtle trade. These centers were located at Baidyar Bazar, Sonargaon; Narayanganj (BIWTA Ghat, Jam Tala, Panchaputi); and Dhaka (Mirpur Section 1 and 10) [Fig. 2].

After seeking information about the export schedule, members of the study group were present physically at the centers observing the packing methods, taking measurements of the turtles exported, identifying and sexing them and also estimating the proportion of each species exported in the consignment. The group members had to face a lot of non-cooperative attitudes from the traders. But patience and interest proved worthwhile and when the traders understood that we are not doing any harm to their trade, they gradually came forward.

At present the first author and two research assistants are working on this turtle trade project. The two export centers located within the metropolis Dhaka, Mirpur Sec. 1 and Sec. 10, are being visited weekly. Turtles are being exported every week and those are being monitored. The other centers are being visited once in a fortnight but it is not possible to check the turtle specimens there. The reason for this is that those centers are located far away and that in all the cases the turtles are packed for export after midnight so that they can be transported to the airport by dawn when most of the airlines are operating to the Far East. Most of these turtles are destined for Japan, Hong Kong, Singapore, Thailand and Malaysia where they are mostly used for food.

Results

Zia International Airport, Dhaka is the only shipping port. The turtles are exported live, packed in bamboo-woven wicker baskets. Two to three individuals weighing about 10 - 12 kg are packed in a single basket but when the specimen is large, it is packed singly. Prior to packing the turtles are washed and cleaned of any foreign material. The sturdy cord which is

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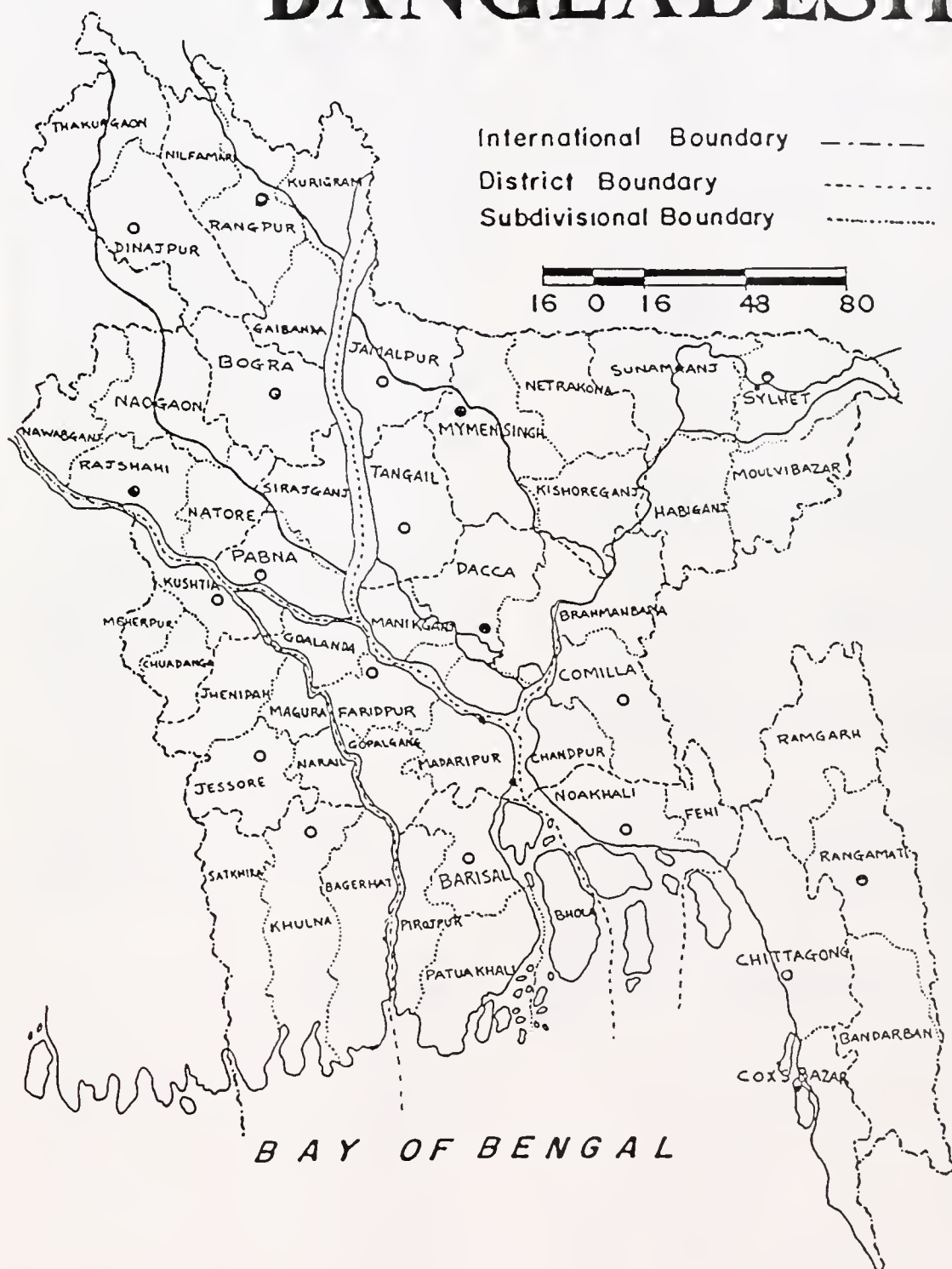


FIG. 2. Regional map of Bangladesh.

used to tie the fore and hind limbs of the turtle on each side together (to restrict its movement) is cut off and then the individuals are placed in the baskets to be packed. The lid is placed over the basket and tied with aluminium wires. The packed baskets are marked with the trademark of the exporter and then transported to the airport. Turtles under 1 kg in weight are not exported. While weighing, packing the exporters do not treat the different species separately.

During this period (summer), the volume of trade is much less. Because of monsoon rain the water level rises and it becomes difficult to catch turtles. But according to some of the turtle hunters the catch is greater because of increased rate of movement of the turtles and the hunters can also maneuver and place traps and other collecting gears in suitable localities. The peak time for exporting the turtles is winter (late October-February). At that time the number of individuals as well as the number of species is higher compared to the summer catches.

Information is being collected about the frequency of catches of the different species in different seasons and also in different habitats.

During this interim period it has been observed that 1 metric ton of live freshwater turtles are exported every week. The volume is much less than during the peak time, in winter, when the volume rises to 5 - 6 metric tons per week. Presently turtles are being shipped once a week but during winter they are shipped almost everyday. The species exported during this period were *Aspideretes hurum*, and *A. gangeticus*. *Aspideretes hurum* comprises the major portion of the bulk followed by *A. gangeticus*. *Lissemys punctata* is not being exported but smuggled to neighboring India with whom Bangladesh shares most of the boundaries. The sex ratio of the exported turtles have been found to be 45.71% males and 54.29% females irrespective of the species. The average weight of the exported turtles was 7.72 kg ranging from 1 kg to 33.20 kg.

From one of the export centers in Dhaka 4017 kg of live turtles were exported from June 10th to August 21st. The ratio of the turtles, in terms of number of individuals were *A. hurum* 71.43% and *A. gangeticus*- 28.57% and in terms of weight was *A. hurum* 83.62%; *A. gangeticus*-16.48%. Assuming that turtle demand for export is the same and that the number of people going for it is also the same, the decline in the export figures during 1987-88 (Fig. 1) can be related to the decline of the turtle population in the wild. There are occasional reports of *Kachuga recta* hatchlings being exported to Japan for pet trade. About 200 hatchlings were exported in 1988, and 40 kilograms of live *Kachuga recta* hatchlings and juveniles were exported to Singapore last year. In June 1989, there was a consignment of 40 kilos of live *Geochlemys hamiltoni* shipped to Singapore.

The prices of the turtles also vary considerably. The collectors sell *A. hurum*, *A. gangeticus* and *Chitra indica* at the rate of Taka 1200 - 1300 per maund (1 maund = 33 kg. approx.) to the middleman (locally known as *maha ian* or *bePari*) who in turn sells it at the rate of Taka 1400 - 1500 to the suppliers, who feed the exporters. The rate of the final exchange between the supplier and the exporter is not known. *Lissemys punctata* is bought at the rate of Taka 500 - 600 per maund from the collectors and sold by the middleman to the supplier at the rate of Taka 700 per maund (1 US \$ = Taka 30). Last year at one time the prices went up to Taka 1100 - 1200 per maund. The meat of the turtles which die off during transportation is consumed locally and is sold at the rate of Tk.50 - 55 per kilogram and that of *L. punctata* Tk. 15 per kg. *Kachuga tecta* is being sold in the country markets at the rate of Tk. 10 - Tk. 15 per kilo. Earlier the money was channeled down by the exporter to the supplier, who gave it to the middleman and finally it reached the collectors. The collectors were committed to the middleman to supply turtles at a rate determined by him. This trend has changed a lot now. The middleman invests his own money and the collectors negotiate to fix the

rate. This is because of the low rate of catches. The collectors complain of the non-availability of the turtles and the middleman has to comply with it.

Recently the working group has been able to contact the airport officials in Dhaka by whom the exact weight of the turtles shipped is recorded. In most of the cases the weight figures measured in front of the group members at the turtle export centers are not the same as the airport figures. The airlines carrying it and the final destination of the shipment will be known. Very often this information is concealed by the exporters. Also the business organizations exporting turtles will be known. So far some of the exporters have been contacted. The Forest Department personnel have also been contacted and liaison is being maintained with them.

Based on the information from the turtle suppliers about the collecting sites, the senior author and research assistants have travelled extensively to some areas in south Bangladesh to see the techniques used to collect chelonians and the habitat from where they are collected. Some of the major supply and collecting areas have been identified. Interviews have been taken of the traders and hunters and collectors. The areas visited thus far are Maijdi, Begumganj, Chandraganj, Lakhipur, Dalalbazar, Char, Alexandar, Ramgoti, Comilla, Laksham, Chandpur, Hajiganj, Sahatali, and Chittagong.

Discussion

Species Involved in Local and International Trade

The freshwater turtles found in Bangladesh belong to the families Trionychidae and Emydidae (Testudines, Reptilia).

Family Trionychidae Subfamily Cyclanorbinae

1. *Lissemys punctata andersoni* (Lacepede 1788), Flapshell Turtle.

Subfamily Trionychinae

2. *Aspideretes gangeticus* (Meylan 1987), Softshell turtle
3. *Aspideretes hurum* (Meylan 1987), Peacock Softshell Turtle.

Family Emydidae Subfamily Batagurinae

4. *Geoclemmys hamiltoni* (Gray 1831), Spotted Pond Turtle.
5. *Morenia petersi* (Anderson 1879), Eyed Turtle.
6. *Hardella thurji* (Gray 1831), Crowned River Turtle.
7. *Kachuga tecta* (Gray 1831), Roofed Turtle.
8. *Kachuga tentoria flaviventer* (Gray 1834), Tent Turtle.

Classification follows Obst (1988). The generic name of *Trionyx* has been replaced by *Aspideretes* and the common English names are used following Stubbs (1989).

There are reports of some of the other species being involved in the trade, like *Chitra indica*, *Kachuga dhongoka* and some others. But during the interim study period, no specimens of these species were observed. This gives rise to a great concern for particularly *C. indica*. In the past this species has been heavily exploited and the hunters and exporters believe that there is a serious decline in its population. *Pelochelys bibroni* was included in the chelonian list by Shafi and Quddus (1977), Husain (1979), and Khan (1982, 1985) but no precise localities were mentioned. Fugler (1984) was also not certain whether this species is included in trade or not.

All the species mentioned above are consumed locally, mostly by the non-moslems. The rate of consumption has increased to a considerable extent, which needs to be monitored.

Species Involved in International Trade

1. *Lissemys punctata andersoni*.
2. *Aspideretes gangeticus*.
3. *Aspideretes hurum*.

4. *Kachuga tecta*.
5. *Hardella thurji*.
6. *Geoclemmys hamiltoni*.

Because of the wide distribution and availability of *Lissemys punctata*, it is consumed on most occasions. Apart from this, a good lot is also smuggled to India. The present investigator detected one smuggling route in eastern Bangladesh. There are reports of some more well established routes in the northwest and southwest Bangladesh. *Kachuga tecta* is also consumed quite often. It is estimated that most of the ethnic groups in the northeast, northwest and southeast consume at least either one *Kachuga tecta* or *Lissemys punctata* per week per household.

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The Past and Present Situation of the Chinese Alligator

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Key Words: Reptilia, Crocodilia, Alligatoridae, *Alligator sinensis*, China, endangered species, history, conservation.

Introduction

The Chinese Alligator is one of 21 species of existing crocodilians in the world today. Their numbers have dwindled and their distribution is so narrow that it has aroused concern among experts, conservationists, and amateurs in wildlife at home and abroad. It is reported in foreign countries that the Chinese Alligator is an extinct animal in the wilderness. It has been placed on the list of endangered species by the International Union for the Conservation of Nature and Natural Resources. How did the Chinese Alligator live? How does it live now? This is a problem of worldwide attention.

Changes in the geographic distribution of the Chinese alligator

The fossils of the Chinese Alligator have been found in Taian and Yanzhou in Shandong Province, Maqian in Shanghai, Yuyao in Zhejiang Province, and Hexian in Anhui Province. In addition, some unidentified fossil alligators have been discovered on the south border of the Junggar Basin in Xinjiang Uygur Autonomous Region; Jiulengshan, Douan in Guangxi Zhuang Autonomous Region; Nanjing in Jiangsu Province; and Danxian in Hainan Province. These fossils reveal that the range of the Chinese Alligator extended from Taian, Shandong Province, to Yuyao, Zhejiang Province during the Neolithic age of the Recent epoch. If the unidentified alligator fossils are included, the range during the late Eocene and the beginning of the Oligocene would have extended from Shanghai and Yuyao, Zhejiang Province in the east, as far west as Douan, Guangxi Zhuang Autonomous

Region to the border of Hainan Island in the south, and to the Junggar Basin, Xinjiang Uygur Autonomous Region in the north.

According to ancient records which can be traced back to 3000 before present, the habitat of the Chinese Alligator was limited to the extensive lake and marshland of the middle-lower Yangtse River, along the banks of the Yangtse River from Shanghai to Jiangling City in Hubei Province, around Dongting Lake in southern Hubei and northern Hunan Provinces, including the extensive river network between the two provinces, and the Shaoxing, south of Hangzhou Bay in Zhejiang Province, approximately 28.5° - 32.5° N, 116.6° - 121.9° E. This range probable continued until the mid-19th century. However, in many regions, the Chinese Alligator became extinct. Reliable records show that they became extinct in the south of Hangzhou Bay in 1201 AD. A great number were killed around Nanjing in the 1870's. The bank of the Yangtse River frequently collapsed, and flooding occurred. It was thought that the alligators picked holes along the bank and caused the disasters. Thus, people killed a great deal of alligators, and drove them to extinction there.

The investigation in the 1950's revealed that the range of the Chinese Alligator stretched west from Pengze in Jiangxi Province, east to the west bank of Tai Lake, the north border of the Yangtse River, and south at the foot of Mt. Huang. To the north of Mt. Dongtianmu, 30.0° - 31.6° N, 118° - 120°E, the range has dwindled. Further supplementary investigations beginning in 1976 proved

that the range became smaller and was limited to ponds of a hilly region to the north of Mt. Huang, below 200 meters in elevation. There were a few individuals that extended northward along the riverside plain, and even as far as the Yangtse River, approx. 30.6° - 31.6° N, 118.0° - 119.6° E. Within this range, they are sparse. The present habitat of the species is mainly located in some villages in Xuancheng, Nanling, Jingxian, Wuhu, Langqi, and Guangde Counties in Anhui Province, and is also situated around a few villages in Anji and Changxing counties in Zhejiang Province, adjacent to the Anhui border. In 1983 the Chinese Alligator's Natural Refuge organized the research workers of several counties to make a survey and statistically estimated that the number of alligators was about 500. Among the 200 animals captured in part by the investigation, and in part by the Research Center of Chinese Alligator Reproduction, only 4.6% were immature, and 95.4% were older than 10 years of age. Thus, the age pyramid was inverted. Other recent investigations on alligator eggs found that the number of eggs has gradually declined in recent years. The Research Center of Chinese Alligator Reproduction obtained 270 eggs in 1982, 278 eggs in 1983, 154 eggs in 1984, and 85 eggs in 1985. The eggs have not only declined in quantity. They also rarely hatched normally. Thus, it is clear that the wild Chinese Alligator population is declining.

Reasons for the dwindling of the range and number of the Chinese Alligator

Climatic change

Fossil alligators were distributed in the Junggar Basin, Xinjiang Uygur Autonomous Region during the late Eocene to the Oligocene. In the Recent epoch, their range extended to the Yellow River. However, in our country it is recorded with reliable authority that there is no trace of them in these regions. This fact indicates that in some regions, the Chinese Alligator has long been extinct. Climatic variations are an important factor, and it is known that

the worldwide climate became cold during ice-ages in the Quaternary period. According to information provided by Jiacheng Zhang, the greater ice-age of the Quaternary period in our country may be divided into six sub-ice-ages and six inter-ice-ages. The yearly average temperature of the inter-ice-ages was 3° - 6°C higher than that of the present, but the average yearly temperature of the sub-ice-ages was 6° - 12°C lower than that of the present. According to records in literature, in 903 BC and 897 BC, the Han River froze twice. In 366 AD, continuous freezing prevailed for three years on the surface of Bohai Bay from Changli to Yingkou. At that time, vehicles, horses, and troops 3000 to 40000 strong could pass over the ice surface. Carriages could pass over Taihu Lake when it was frozen in 1111 AD. The Chinese Alligator is an animal that is adapted to warm weather and not to cold. Late hibernation is an important period, then the reproductive organs develop. At low temperatures, reproduction cannot proceed normally. The hatching stage is about one month, and requires a temperature of about 30°C. If it is lower than 28°C, the young can hardly hatch. Thus it is certain that it is difficult for the Chinese Alligator to proliferate in chilly regions. They can only occupy the area south of the Yangtse River because there is a cool climate to the north.

Habitat destruction, the most important factor

The Chinese Alligator likes to live in water habitats such as ditches, ponds, reservoirs, etc. These habitats accumulate water year-round. These provide a mild and damp climate. Grass and trees grow luxuriantly, and numerous species of animals are common. This environment enables the Chinese Alligator to not only procure food, build holes, and mate in the water, but also to build nests and produce offspring on land. In the course of thousands of years, it was here that people reclaimed wasteland and built water conservation projects. Artificially cultivated plants were grown instead of natural vegetation. The alligator's holes

and nest-sites were destroyed extensively. All of this resulted in reduction of range and population size. We have investigated the habitat of the Chinese Alligator in the villages of Wanchun and Yitai, and the town of Qingshuihe on the outskirts of Wuhu. At present, there is level and open terrain with a vast extent of farmland, numerous villages, and well-developed roadways. The Shuiyang River lies to the east, flowing westward where it meets the Yangtse River. The Chinese Alligator is extinct in this region, which was altered radically about 80 years ago. Beach used to stretch for tens of miles along both sides of the Qingyi and Shuiyang Rivers. When the tide ebbed, reeds and other plants were exposed, providing habitat for many varieties of animals. When the tide was at flood, alligators were common on remote beaches in sparsely-inhabited areas. From the late 16th to the early 20th centuries, people from the north of the Yangtse River moved into this area, and began to cultivate an increasing amount of beach land.

The Wanchun Embankment was built in 1904. When a dam was being built, alligators were common around the flooded plain. When a dam was completed, they still inhabited ponds, pools, and ditches within the dam. As the alligators dug holes and built dens, they often destroyed the dam, flooding seedlings, and endangering fish and ducks. Peasants made a point of hunting Chinese Alligators whenever they were discovered, and the number of individuals living in the embankment has declined. However, on the plain that had once been flooded, where the Shuiyang and the western Qingyi rivers meet, a great number of Chinese Alligators survived. In 1927, people began to build a dam at this spot. The Yitai Embankment was completed in 1931. Farmland and villages replaced the beach. Within the memory of the former generation, "Chinese Alligators could be heard roaring everywhere in summer -as much as frogs are heard croaking- echoing the whole neighborhood". It was here in 1935 that Z. D. Xiao conducted a study and described the state of the Chinese Alligator. There were a number of the animals in this region

then. C. G. Zhu (1951-1956) made an investigation in the same region and only discovered alligators in Wuhu. This region was a desolate beach then. In 1954 I captured one alligator and made it onto a specimen. It has been preserved in the Department of Biology, Anhui Normal University. In 1959, the Wanchun floodgate was built to irrigate farmland. In the meantime, people built a complete set of engineering equipment and an irrigation canal. All Chinese Alligators were dug out and killed. The area became farmland, and the habitat of the Chinese Alligator was destroyed. A large-scale drive to eradicate the blood fluke was launched in 1958. A large amount of sodium pentachlorophenate was applied to the river basin. The last alligator at Yitai Village was poisoned. During the twenty-odd years that followed, Chinese Alligators and their sign were not found. The Qingshuihe River is only an example. Other locations met the same fate but in various degrees. People have multiplied considerably in the present range of the Chinese Alligator. They weeded all corners to get brushwood burnt. When alligators began to build nests and hatch eggs, sufficient weeds were needed. The weeds grew less and less, and in 1984 only one alligator deprived of a nest was captured by a peasant.

Due to the fact that vegetation was destroyed, the areas of water in reserve had sharply dropped, and the area of wasteland to reclaim had greatly increased. The ponds and ditches that have never dried in history show frequent droughts at present. Moreover, because the forests have disappeared, soil and water cannot be conserved. There are rivers that flow into the Yangtse River (e.g. the Qingyi, Shuiyang, and Zhang rivers) whose beds have risen 1-2 meters in height, and have frequently flooded. Flood and drought have rendered the alligator's livelihood exceedingly difficult. When habitats incurred drought and flood, the alligator had to move away from the dry land or the submerged holes and look for habitat elsewhere. They were often captured or killed during the process of moving.

Excessive, indiscriminate capture or slaughter

Chinese Alligators are often killed because they consume fish, ducklings, and small geese, and damage dams by digging holes. Thus they damage things that are of immediate benefit to people. Another significant factor is that the alligator supplies edible meat, useful skin, and medicinal materials. So, excessive and indiscriminate capture and slaughter has not been rare in the past, and remains common in the present day. For example, *Guoxianjiayou*, a book written during the reign of Jiajing in the Ming Dynasty, records:

The bank of the upper Yangtse River near Nanjing often collapsed during the early years of the Ming Dynasty. It was due to this reason that the Chinese Alligators had herein drilled holes. It was reported that there was an old fisherman who had once said: 'Roast dogs were used as bait, put a hook; by raising the bait, you trapped alligators'.

The above record was not mentioned in the history of the middle Ming Dynasty, which verified the fact that after excessive harvesting during the early years of the Ming Dynasty, Chinese Alligators living in the Nanjing area had become very scarce. The *Classical Chinese Materia Medica*, written by S. Z. Li, recorded the medicinal value of Chinese Alligators, and their meat was served as favorite dishes at wedding feasts. All these serve to verify that catching alligators was in great vogue at that time. After going through the great disaster of catching and killing during the Ming Dynasty, the alligator's population was reduced, and its range dwindled rapidly. During the Qing Dynasty, the government began to divide land into regions to provide cattle ranches for the Mandarin. For example, Wanchun Dan in Wuhu district was an area of land reserved for cattle ranches. People were forbidden to plough or sow in such land so that wild grass could grow densely. Such reservations gave alligators fine conditions for prolific reproduction. But the custom of killing alligators continued. Peasants not only caught alligators by using fish hooks, but developed a new device of

string bows set around the burrows. As soon as the alligators emerged, they were trapped.

Application of large amounts of chemical fertilizers and insecticides in the field

Alligators feed on snails, mother-of-pearl, shrimp, aquatic insects, fish, frogs, turtles, birds, and small mammals. Among these, aquatic animals are their chief food. Since a great quantity of chemical fertilizers and insecticides have been applied to farmland in recent years, the growth of the fish, shrimp, and mothers-of-pearl is affected when the polluted water flows into ponds. So, the decrease of natural food has greatly influenced the reproductive success and survival capacity of alligators. It is common for young alligators to die during the winter season due to insufficiency of food.

Protection and captive breeding of the Chinese Alligator

In order to ensure the survival of the Chinese Alligator, the Forestry Department of the China National Government, and the Anhui Provincial Government have taken two measures.

1. Conservation

The first measure (in 1980) was to set up natural conservation effort for the species. The main goal was the protection and enlargement of the existing Chinese Alligator population and the protection of their habitat. Thus, a unit of leadership was established in the project which covers five counties with their respective species-protection work units. Reported here is the conservation effort:

In order to observe and investigate the location and population size of the species, the conservation workers in each county employ identical approaches. They inquire with the local folks, explore caves, and calculate statistics using headlamps. Every possible water habitat is examined. Since alligators have stationary territories, observation in the field is convenient. A

stock of information resulted from the project, and provided valuable data for the development of the species.

Through legislative measures, the National Government has ruled that the Chinese Alligator is a first-class rare animal to be conserved and protected. Hunting is not allowed. According to Item 130 of the National Offense Law, those who break hunting regulations by hunting in a restricted region, during a restricted period, by forbidden means, or harm rare animals, will be sentenced to two years in prison, or be subject to a heavy penalty. These regulations are strictly enforced by the police, who exercise their mission to keep the dignity of the law.

It is openly advocated that the Chinese Alligator is one of China's rare and valuable animals, and belongs to our national resources. Local folks are enlightened and therefore change their view of the Chinese Alligator as a harmful species. Folks are also made to recognize the great significance of the Chinese Alligator in academic research and its considerable economic benefits. Thus, everyone begins to be concerned about the species, and protects it. The provincial and local governments also post notices to inform the public that protection of the Chinese Alligator is rewarded, while the killing of the species is punished.

A full consideration of spatial and temporal factors strengthens the effectiveness of the conservation effort. Because the alligators presently have a fragmented distribution, their conservation is negatively affected by overcrowded human habitats with their large stretches of farmland and weaving highways. Considering these factors, many conservations stations are set up in the conservation area. If alligators are spotted in their caves, a conservation station is immediately set up with someone (usually a local farmer) who is responsible for the station and is paid from a special fund from the National Forestry Department. As the conservation station, no one is allowed to use chemicals, to cut grass, or to ravage the

alligator nests and eggs. Consequently, the alligators in the conservation area enjoy proper protection. In some areas, alligators obtain the necessary conditions for reproduction, such as in Xuancheng, Nanling, and Jingxian counties, where in the past two years, alligators have been seen nesting, laying eggs, and hatching young. The alligator population in these areas is recovering and increasing in size.

2. Research

In order to achieve the rapid and effective recovery of the Chinese Alligator population, the second measure taken by the Forestry Department and the Anhui Provincial Government was to set up the Anhui Research Center of Chinese Alligator Reproduction in close cooperation with the Department of Biology, Anhui Normal University. Here, a thorough study of the ecology of the species has been made. This has resulted in a systematic theory to be applied to captive breeding and artificial reproduction. Currently, the artificial incubation of Chinese Alligator eggs, and the raising of the young alligators has had much success. Details are reported as follows:

Pen construction. A pen for alligators should be located in quiet marshy areas with appropriate temperatures and rich sources of food. After the location is decided, pens must be constructed with walls of brick, stone and cement. The height of the walls should be over two meters. When the rainy season comes, the walls may be surrounded by standing water, so the foundation should be 1.5 m below ground level, so as to keep the alligators from escaping by digging. The pen pond should be planted with trees and bushes, making it possible for the alligators to nest under the cover of vegetation. The land should be scattered with wild seeds to provide the necessary grass for nesting. The depth of the pond water should be kept at 0.5 m or more. Within the pond, small islands are built, where the alligators can enjoy sunshine.

Captive breeding. Captive breeding efforts

must take into account such biological factors as sexual maturity, courtship, copulation, nesting, and hatching. At different stages of growth, alligators have different requirements as to the quality and quantity of food. At sexual maturity, alligators need many kinds of substances, so food should be prepared with variety. During courtship and copulation, when they are stimulated by sexual hormones, both males and females are very active, and will often fight for a sexual partner. Males and females should be grouped on a ratio of one male with three to five females. The water depth should meet the requirements of activity and copulation. For constructing nests, large quantities of grass should be provided in the reproduction areas, so as to provide sufficient nesting materials for the gravid females, and to prevent fighting, harmful interactions, and decrease in egg deposition. During the entire period of reproduction, female alligators must be kept in extreme quiet in order for them to perform. As the alligator's appetite is slightly decreased by the process of reproduction, feeding should be monitored. After egg deposition, alligators begin to eat more, and the usual level of feeding is resumed. Overfeeding is to be avoided, lest the alligators gain too much fat, which affects their health and lowers reproductive productivity. During the winter, more care should be given, and all alligators who have not entered their caves before hibernation should be captured and sent to artificial hibernation chambers.

Egg deposition of captive alligators. Given the above requirements, captive alligators can lay eggs normally. The adult captive alligators we bred laid 264 eggs in 1983, 503 eggs in 1984, 809 eggs in 1985, 801 eggs in 1986, 1045 eggs in 1987, and 1219 eggs in 1988.

Artificial incubation of alligator eggs

Construction of incubation chambers

The incubation of alligator eggs requires high temperature and humidity. In constructing incubation chambers, enough

emphasis should be placed on temperature and means of raising temperature. The surface of the chamber walls should be waterproof. The walls and floor should allow for cleaning readily. The incubation chambers at the Chinese Alligator Research Center have a double glass roof, and a double glass wall that faces south. Temperature is controlled by the temperature-controller. The incubation chambers should not be too spacious, so as to save energy and allow for easy control.

Equipment for incubation

Make a round egg collector and a square incubator which can let water go through at the bottom, to keep the eggs from being suffocated by the standing water at the bottom. Plants which can help stabilize temperature and humidity, and allow for ventilation, best serve as the filling of the incubator. The research center finds that moss is a very good filling material. The search is continuing for better fillings. The chamber temperature is generally controlled and monitored by means of electricity.

Techniques of incubation

1) Immediate collection of alligator eggs is required, as too many alligators in the reproduction area can possibly get the eggs crushed if not collected in time.

2) Egg collectors are used in collecting eggs. Quick action is required, and attention is to be given to the natural order of the eggs. The alligator eggs are stacked in baskets according to their natural order, and are sent to the incubation chambers immediately. Try to avoid shaking as much as possible in carrying the eggs.

3) Incubators and incubation chambers should be kept clean and be adequately sterilized to avoid bacterial or viral infections.

4) Alligator eggs are often in multilayer order when discovered in the wild. Artificial incubation requires monolayer arrangement.

5) Incubation temperature should be maintained at about 31°C. Humidity for the first four weeks is 95%. Use 85-95% humidity for the rest of the incubation period.

Raising young alligators

The mortality of young alligators is high in the first year, thus the key to breeding is the successful raising these juveniles.

Construction of cages

Cages for young alligators have requirements identical to those of the incubation chambers, as well as ventilation, sunlight, and adequate water and drainage.

Methods of raising hatchlings

The time between pipping and breakdown of the shell varies from a little over an hour, to two to three days. Hatchlings slow in liberating themselves are often poor in health, so they should be taken good care of. The hatchling has a crack 1.3-1.5 cm long in the vent in which some unconsumed yolk remains. This continues to provide sustenance for the hatchling, which needs no food during its early infancy. When to feed the hatchlings is still being studied. The newly-hatched alligators can be kept in the cage with enough area of water and dry sand and stone for the alligator to move about freely. Water supply and sanitary conditions are a significant factor in survival rate. Consequently, daily cleaning is required to remove food remains and excrement. When the hatchlings need to be fed, some *Oryzias latipes* can be thrown into the cage alive. Hatchlings in dry areas can be fed with fish meat in a small saucer, or with artificially-prepared food. Hatchlings are especially greedy; however, too much food can give rise to gout. If hatchlings are found in low spirits, tired of eating, or suffering from paralysis of the legs (a symptom of gout), feeding should be stopped immediately.

Soon after the hatchlings liberate themselves from the shell, the weather gets

cool, which could reduce their appetite. Now, the temperature should be raised. The temperature in the cage must be maintained at approximately 31°C. The hatchlings will recover their appetite and will gain weight rapidly. In fine weather when the temperature rises to its normal level, hatchlings should be given more of a chance to enjoy sunshine. Individual differences in growth rate will be evident by now, and the young alligators should be grouped accordingly. In the area around the cages it is desirable to keep quiet, cut down human interference, reduce the possibility of infection by pathogens, and to reduce the possibility of predation on the alligators by mice. When the young alligators grow as weighty as 40 g, they can be sent into hibernation. Two or three days before hibernation, feeding is stopped so as to avoid diseases and ailment caused by food left in the digestive canal when temperature is lowered. It is desirable to reduce the temperature gradually until all food is completely digested. Temperature should be lowered by 2-3°C each time. Below 20°C, a larger decrease is allowable. 10°C is the proper hibernation temperature. Hibernation chambers can be set up underground, at a temperature of 10-12°C, and at 80% humidity. Late in hibernation, bowls of fresh water are supplied for the young alligators.

To conclude, our breeding techniques generally agree with the natural growth of young alligators in the wild. Consequently, the population rises year by year. The number of surviving captive-bred Chinese Alligators is as follows: 66 in 1982, 77 in 1983, 117 in 1984, 300 in 1985, 450 in 1986, and 975 in 1987.

Acknowledgments

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Book.

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Abstract of oral presentation

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Moody, S. 1980. Phylogenetic and historical biogeographical relationships of the genera in the Agamidae (Reptilia: Lacertilia). Ph.D. Thesis. University of Michigan. 373 pp.

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C. C. LIU 1900-1976

This volume of Asiatic Herpetological Research is dedicated to the memory of Cheng-chao Liu. This year is the 90th anniversary of his birth. C. C. Liu, China's most eminent herpetologist, was the author of 55 papers and two books on herpetological subjects. Liu died in Chengdu, Sichuan, China on 9 April 1976.

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